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# UNDERNUTRITION IN STEERS

## ITS RELATION TO METABOLISM, DIGESTION, AND SUBSEQUENT REALIMENTATION

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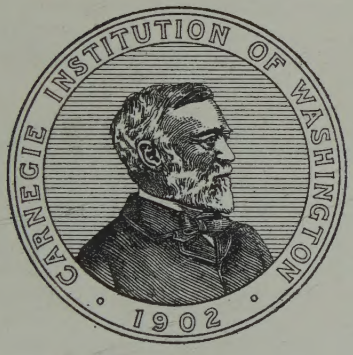
By Francis G. Benedict and Ernest G. Ritzman

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# UNDERNUTRITION IN STEERS: ITS RELATION TO METABOLISM, DIGESTION, AND SUBSEQUENT REALIMENTATION.

By F. G. Benedict and E. G. Ritzman

From the Nutrition Laboratory of the Carnegie Institution of Washington, at Boston, Massachusetts, and the New Hampshire Agricultural Experiment Station, Durham, New Hampshire.

With forty-two text figures.

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# INTRODUCTION AND CONSIDERATION OF BASIC CONCEPTIONS.

During the period of stress of the Great War attention was repeatedly fixed on the importance of conservation of food resources and, to a certain extent, on the possibilities of curtailing the food intake at certain stages of animal and human life. This latter consideration led to a number of physiological observations on men, partly of laboratory and partly of a nation-wide nature. The final conclusions were that with adult humans a considerable curtailment in food intake may obtain for many months without serious, permanent detriment, and that the safety factors of the animal body are so great as to permit complete recuperation after a prolonged period of submaintenance food intake, although even now it is not settled as to how long such underfeeding can be carried out with man with full recuperation still possible. Extensive experience in the complete withdrawal of food for both short and long periods with men showed clearly that such withdrawal was not especially distressing and certainly left no demonstrably injurious after-effects. It can be safely stated that a complete withdrawal of food of from two days to a week is not injurious to the human organism. Indeed, one observation where the subject was studied during a 31-day fast showed a phenomenal retention of physical and mental powers, with ultimately complete recuperation. Based upon these extensive experiences with humans, it seemed not inadvisable to attempt observations on large domestic animals, with a primary object of noting the influence of prolonged undernutrition upon the physiology and general welfare of such animals. Entirely aside from the profound physiological interest attached to such a study of undernutrition is the fact that the great economic problems attending beef production are in the last analysis closely interwoven with scientific feeding, and we have as yet only an incomplete answer to the question, *What is scientific stock feeding?* In the light of our studies with humans, information as to the effect of undernutrition, if not indeed complete fasting, in beef animals is certainly essential to a full knowledge of the science of feeding.

The commonest rule in practical as well as in supposedly scientific livestock feeding implies that a most liberal provision of food under any and all conditions (i. e., maintenance, growth, and production) is a prime requisite of good management and a procedure essential to profit. While this seems to have been a sound rule during our earlier period of overproduction in crops, and applicable especially to the corn-belt sections of our country, it is becoming increasingly clear that its application to conditions with less prolific indigenous feed supplies must be open to severe criticism.

It is axiomatic that the finished animal products can be transported to market much more cheaply than the raw products (hay, fodder, and concentrated feeds) required to produce them, and it therefore follows, as a logical corollary, that such feedstuffs can be most economically converted into animal products in the section where they are grown, where there is the least handling, and (what is of even greater importance) when subjected to the least possible trade manipula-

tions. Hence, in the less-favored grain-producing sections of our country the feeding of beef cattle has become an expensive proposition, and the high cost of the feed can be compensated for only by methods of economy in the feeding of the cattle. Animal products are a much more costly form of human food than the cereals from which they are produced, due largely to the caloric losses in converting plant into animal tissue. Hence, under stress of general food shortage man is usually forced to forego the meat in his diet and in its place to consume the cereals from which meat is ordinarily made, because these yield a larger sum total of available calories. As a result, as human population becomes more dense, livestock meets with rather severe competition for its position as the chief source of concentrated food supply and, consequently, the problems of animal nutrition assume quite a different physiological as well as economic aspect from those of our pioneer condition. That we are now undergoing such a transition is very evident on close observation, and it would seem highly advisable that research should meet the new problems in their true economic light.

In such modernized considerations not only is a more thorough realization of the use of food and of the adequate husbanding of its resources by proper use involved, but perhaps, as a primary requisite, as great attention should be given to the physiological susceptibilities of the animal itself to function as a machine under the various exigencies of food-supply. Only recently has methodical curtailment of food as a conceivably sound practice received consideration in America. A strong tendency has always existed towards wasteful feeding. But recent investigations on the presence and function of various accessory food products, the so-called "vitamines," suggest that due regard for quality and choice of food might often have resulted in great savings in the quantities fed, since a poor choice of food is simply waste. Other physiological studies on animal behavior on curtailed rations indicate that mere quantitative curtailment systematically managed may be safely resorted to, so far as health and recuperation are concerned.

During the Great War, when national measures were put into force in practically every country, regulating more or less the food intake as a means of conservation, food restriction naturally played a very great rôle, and subsequent history has shown that little, if any, harm has resulted from it, save where food restriction amounted to a profound starvation. If domestic animals possess an equal amount of reserve power and an equally efficient recuperative capacity to that shown by human beings, this fact might, under certain circumstances, serve a useful purpose in feeding animals and would certainly serve as a groundwork for a revision of the standards of animal nutrition. The economic aspects of the problem, while not determining the research scheme, were of such general interest as to warrant a cooperation with the joint resources of the Nutrition Laboratory of the Carnegie Institution of Washington and the Agricultural Experiment Station at Durham, New Hampshire. It is our purpose in this report to present a series of observations carried out on large domestic animals (steers) with regard to the effect of prolonged undernutrition. The main problem was to study the influence upon animal physiology of submaintenance and subsequent realimentation, but other subsidiary problems of physiological and, indeed, of probable economic interest were considered in the two-year program here reported.

Hitherto, practically all considerations of the economic aspects of animal nutrition have been based upon the fundamental belief that there should invariably be most liberal rationing for maintenance as well as for growth and for animal production. For the development of growing animals and for the maintenance of milch cows little need be stated with regard to the importance of providing most liberally for growth and for milk production, growth in this sense referring to prenatal as well as postnatal growth.

Although the influence of undernutrition forms a rather necessary link in the study of food utilization and its physiological reactions, in general practice it has seemed unwise, undesirable, if not indeed unlawful, to underfeed designedly a domestic animal. This type of public opinion has no doubt resulted from the fact that such practice has, in our past history of "bumper" crop production, been unnecessary and, in fact, uneconomic, and where found it has largely been due to a common drift of shiftlessness, lacking objective or the requisite methods of control and protection. Before drawing too stringent conclusions with regard to either the economics or the ethics of the underfeeding of domestic animals, it is important to consider what is the normal course of nutrition with many of the wild animals. Wild animals, depending as they do upon food material subject to adverse seasonal and climatic conditions, the ravages of insect pests, and scant rainfall, find it necessary in a large majority of instances to migrate extensively in order to insure food for maintenance. The migratory birds pass many days, if not weeks, without appreciable food-supply. A full-grown goose can readily go without food for 30 days without showing any apparent detriment.

Parker[a] has pointed out the remarkable changes in nutritional level of the bull seals in the Pribilof Islands. At the beginning of the mating season they are in physical prime, but throughout the entire season no food is taken and the animals are engaged in fierce physical combats. Thus at the end of the breeding-season the animals are in a distinctly depleted muscular condition. Returning to the sea, they feed and fatten in preparation for the coming season. With the cold-blooded animals this period of abstinence from food may be incredibly extended. Thus, there is a well-authenticated instance in the case of a large python at the New York Zoological Park that went over 20 months without eating, subsequently took food, and lived many years. The observations of Miescher,[b] and particularly of Greene[c] and of Clark and Almy,[d] show that during the breeding-season salmon fast for many months.

From these and innumerably similar incidents it is clear that with most wild life there are periods of normal sustenance corresponding to the maintenance periods with our animals, there are periods of very scant rations corresponding to our submaintenance periods, and there are periods of plethora, usually in the late vegetative growing season, corresponding to our fattening periods. Thus, in a sense, our experimental program is reasonably comparable to the feeding conditions of many wild, herbivorous animals, especially

[a] Parker, Scientific Monthly, May 1917, p. 393.

[b] Miescher-Reusch, F., Statistische und biologische Beiträge zur Kenntniss vom Leben des Rheinlachses im Süsswasser, Internat. Fischerei-Ausstellung, in Berlin, 1880, p. 154; see also Miescher-Reusch, Die histochemischen und physiologischen Arbeiten, Leipsic, 1897, p. 166. Cited by Clark and Almy, Journ. Biol. Chem., 1918, **33**, p. 497.

[c] Greene, Journ. Biol. Chem., 1912, **11**, p. xviii; see also same journal, 1918, **33**, p. xiii.

[d] Clark and Almy, Journ. Biol. Chem., 1918, **33**, p. 483.

the ruminants, such as deer, elk, moose, goats, and bison. From an analysis of the food habits of wild animals, therefore, it would appear that neither short periods of complete abstinence from food nor, indeed, long periods of undernutrition are distressing or permanently damaging to health.

These deductions from the food habits of wild animals find strong supporting evidence in relatively recent experiences with men. One must disregard, in this connection, most of the evidence from the European nations in their several distressing food crises, for other conditions than inadequate diet are continually met, such as disrupted families, lack of coal and proper fuel to heat the house, complete economic reversal in business life, and psychological depression on every hand. Whatever complications may arise in drawing deductions from complex national situations, clear-cut, well-planned laboratory experiments exist to indicate the effect of prolonged undernutrition upon adults. Jansen,[a] Zuntz and Loewy,[b] and the Nutrition Laboratory[c] have made such studies under most restricted diet. The last cited dealt with a group of 25 college students who underwent a severe reduction in diet for several months without detriment or distress. The findings are quite in line with those noted in the European laboratories.

If, therefore, it is possible for a man to fast for a week or even longer without injury, if a group of college students can subsist for 4 or 5 months on one-half their previous normal caloric needs, if thousands, if not millions, of people in Asia and Central Europe can exist on greatly lowered food intake (although in the latter case, daily deaths, lowered capacity for reproduction, increased susceptibility to disease, and disorders of malnutrition are continually and extensively noted), it is reasonable to assume that the time-honored belief that domestic animals should be fed continually and fed to excess may fairly be challenged on two grounds: first, that the complete withdrawal of food for a few days is not injurious or distressing; second, that reasonably prolonged underfeeding is not distressing or permanently injurious.

The ever-present demands during the period of the Great War, not only for the conservation of the foods usually consumed by humans but, particularly in Europe, for the conversion of much material formerly fed to domestic animals into a form suitable for humans, made it necessary to provide other animal feeds. *The possibilities of reducing, temporarily at least, the amount of feed consumed by certain domestic animals seem not to have been extensively considered.*

The feed requirements of beef and dairy animals necessarily vary greatly, depending upon the ultimate end of feeding. The milch cow serves two purposes: first, to produce milk for human consumption; second, periodically to produce offspring. The transformation of coarse food material into human food is most economical in the case of milk production, but the use of the beef animal to convert hay and grasses into flesh for human consumption has developed into one of the greatest food industries. The feeding problems and the end results in a steer are quite different from those in the milch cow. The product is slowly formed, the sale is made but once, and often the trend

[a] Jansen, Deutsch. Arch. f. klin. Med., 1917, 124, p. 1.
[b] Loewy and Zuntz, Berl. klin. Wochenschr., 1916, 53, p. 825.
[c] Benedict, Miles, Roth, and Smith, Carnegie Inst. Wash. Pub. No. 280, 1919.

of the market must be considered. If ultimately the steer can economically convert a certain mass of otherwise unavailable vegetable carbohydrate and vegetable protein into edible fat and flesh, he has served a useful purpose.

Our research deals exclusively with the feeding of beef steers, particularly with curtailed rations.[a] As with the wild animal during the period of rapid vegetative growth, in the summer the steer finds plenty of food in the pasture and hence secures his supply of body material at a minimum cost, but during the winter, as he may not migrate to other growing areas, the farmer must supply his needs for maintenance and growth from the supplies which he has stored at considerable expense, either in labor or by purchase. It is most important to analyze closely this cost to the farmer in food material and labor in wintering the beef animal. The steer is burning up a great deal of feed material. Furthermore, considerable labor by man has been required for the harvesting and storing of this feed. To be sure, this feed is not necessarily taken directly away from man for, in the form of hay, silage, etc. (as ordinarily fed), it is not available for man, but it must still be considered that the same feed could be elaborated by the milch cow into human food. Consequently the steer, throughout the winter at least, is consuming a considerable amount of material that might through milk production be converted into human food more economically. If sufficient feed is given to produce gain in weight, that portion converted to beef flesh and fat is to a certain extent to be considered as salvaged for the use of man. There is always a certain relationship between food intake and fat and flesh deposit. The larger the food intake, in general the larger the deposit of flesh. But, after all, the main expense of winter feeding is *primarily just to keep the animal alive.* Hitherto it has been considered that if the animal is well fed, laying on flesh, he is accomplishing his object in life, but in reality this is accomplished at a cost relatively too high in winter. In order to lay on flesh the animal must be living on a high nutritive plane—that is, with a plethora of feed. The extra cost of flesh production is commonly avoided by feeding just for weight maintenance.

In our diet-reduction experiments with 25 college men, it was found that with one-half the usual amount of food they lost weight, but after full diet was given they not only regained their lost weight rapidly, but continued to gain for some time thereafter, thus suggesting that the period of undernutrition might, under properly controlled conditions, actually stimulate the rate of

[a] It is probably only in the extra feed requirements of cows during gestation and lactation and in the intense growth needs that food scarcity may be seriously injurious. Indeed, while in general it would seem that during the process of growth the withdrawal of food would be particularly damaging, it must be borne in mind that the capacity to grow is apparently never lost. This has been most clearly shown in many of the observations on white rats carried out in the past decade in connection with the interesting study of the absence of so-called "vitamines" and certain mineral constituents in the diet. What is of special significance in connection with the experiments on white rats is that here we have an instance of animals that are literally half-starved, for they do not grow more than half their normal size. With the inclusion of proper accessory substances full growth is attainable. With cattle a remarkable series of experiments was instituted by H. J. Waters, in which it was shown that submaintenance rations with immature animals did not alter skeletal growth. (Waters, Expt. Sta. Univ. Missouri, "The capacity of animals to grow under adverse conditions," Proceedings 29th Annual Meeting Society for Promotion of Agricultural Science, Washington, D. C., 1908, p. 71; also Waters, Expt. Sta. Univ. Missouri, "The influence of nutrition upon the animal form," Proceedings 30th Annual Meeting Society for Promotion of Agricultural Science, Portland, Oregon, 1909, p. 70.)

weight increase when liberal food was again available. Thus, in the case of beef animals, it becomes an economic question of great importance as to whether, when feed is scarce, as in winter, it is not possible for an animal to live temporarily on a considerably lower nutritive plane, under unusual stress of food shortage, even to the extent of losing some previously stored body material, and then in spring and summer when feed is plenty, resume feeding under such conditions that the proportion of gain to the cost of living may be even greater than usual and, indeed, even enough greater to overtake and more than make good all the losses incurred with underfeeding. This, then, is the working hypothesis upon which the investigation we purpose reporting was outlined, based primarily upon the Nutrition Laboratory's experience with a large group of college students. The absence of real distress or appreciable intellectual and physical detriment as a result of the greatly lowered food intake, and the rapidity of the subsequent regain of weight suggested the entire research.

It is important to emphasize that this research was not a study of fasting. Complete withdrawal of food means always a continuous draft upon body reserves, never a balance. Inasmuch as there is no intake whatsoever during complete fasting, all of the energy necessary to sustain life must come from previously stored material. It is conceivable that with submaintenance rations there may be a disposition for the body to adjust itself to the intake either completely or partially; or that while there still will be losses, these losses will be only relatively slight and the whole plane of nutrition may be so lowered as ultimately to strike a balance, where the diminished food intake suffices to maintain life at the lower nutritional level. Under these conditions, therefore, it is clear that the cost of living, which plays such an important rôle with the farmer in sustaining his animals through the winter, may possibly be reduced, even as during the war householders found it possible to reduce the cost of heating their houses. They burned less coal, used less light, and shut up some of the rooms in the house. To be sure, the house was not used to full capacity, but still it remained an abode, a home, easily capable of expanding to its original capacity and usefulness, when plenty of fuel was available. Does such a condition exist with the steer? Is it possible to reduce food intake materially, thus diminishing the drafts upon the grain-bin and hay-mow during the period of the year when feed is costly? Is it possible to do this without too great a sacrifice of previously stored body material in the steer; and finally, when feed is again plentiful, is it possible for the animal to rehabilitate itself and utilize the excess feed for further gains in weight, so that ultimately it will have attained its market condition on a somewhat better economic basis?

It is seen that the problems divide themselves naturally into two phases, first, those that are purely physiological, and, second, those that are economic. The Nutrition Laboratory's published researches deal primarily with the nutrition of man and have not thus far been expanded into reports of studies upon the nutrition of other animals. The importance of the steer in the food of man, on the one hand, and secondly, the intense physiological importance of the possibility of materially changing the nutritive plane of animals other than man (animals that might ultimately be studied over periods of years, while thus far the experiments on man have been only for months), made it perfectly justifiable to enter into this cooperative study, to be conducted from

the standpoint of pure physiology alone. The potentialities of the economic aspects of the question made it particularly advantageous for the experiment station at Durham, New Hampshire, to cooperate in these investigations.

## SPECIFIC PROBLEMS.

### Physiological Problems.

Too little evidence is at hand with regard to the influence of the nutritive plane upon the life habits, particularly the basal metabolism, of beef animals, and our first problem was to study the influence of a pronounced submaintenance ration upon basal metabolism—that is, what are the changes in vital activity in its manifold expressions, resulting from a pronounced depletion of feed? Previous experiments with groups of college students indicated that this method of attack was perfectly feasible.[a] Of the various physiological activities, perhaps the most important is the basal metabolism—that is, the heat-production during approximate muscular repose and preferably without food in the intestinal tract, or at least not during the active period of digestion. Basal metabolism represents the energy expenditure of all the several activities which go to make up the animal life. The muscular movements, external and internal, glandular activities, muscle tonus, are all pooled in the basal metabolism. Hence a measurement of the total heat-production or the gaseous metabolism during any given period will give a measure of the sum of the total activities representing the basal or minimum metabolism. With animals, and especially with steers, the conditions under which the basal metabolism of humans is measured can not be maintained. With man the basal metabolism is supposed to be measured, first, under complete muscular repose, second, 12 hours after the last meal or in the so-called "post-absorptive" condition, i. e., after actual digestion has ceased. With steers and with ruminants in general the experimental conditions for the post-absorptive metabolism are difficult to carry out. At the time these experiments were made, there was almost no evidence with regard to the actual effect of fasting a large domestic animal. The only record in the literature which we have been able to find is that of the steers of Grouven.[b] It is impossible to control the muscular activity of a large animal of this type. Consequently, we had to approximate the conditions representing basal in humans and obtain a metabolism which is not, strictly speaking, basal, but more properly should be designated for the purpose of this research as the "standard metabolism." This, as a matter of fact, was determined not with the animal in complete muscular repose, but standing and with a reasonable degree of repose. Secondly, we did not withhold feed from these animals for a great length of time. The gaseous metabolism was usually measured about 24 hours after the last feeding, a time that does not, indeed, represent complete fasting, but does avoid the "peak" of active digestive processes.

Changes in animal condition are more commonly observed and expressed by the stockman by changes in body-weight than by any other factor, but in immature animals alterations other than weight, such as dimensional

[a] Benedict, Miles, Roth, and Smith, Carnegie Inst. Wash. Pub. No. 280, 1919.

[b] Grouven, Physiologisch-chemische Fütterungsversuche. Zweiter Bericht über die Arbeiten der agrikulturchemischen Versuchsstation zu Salzmünde, Berlin, 1864, pp. 207, et seq.

changes in certain circumferences and in length, are also a necessary accompaniment of any investigation on the influence of reduced rations upon vital activities. Another index of physiological activity is the pulse-rate, a factor which has been almost entirely unobserved in animal nutrition. A study of pulse-rate is imperative in the light of the relationship frequently noted with humans between pulse-rate and metabolism. The degree of body repose is of importance, not only as indicating suitable periods for the comparison of the gaseous metabolism, but particularly the general nervousness or irritability of the animal itself. The technique for recording graphically these activities is described later. Measurements of rectal temperature and skin temperature, particularly the latter, are additions to observations on basal metabolism that are essential in modern experiments. Rectal temperatures are frequently reported throughout the literature, but relatively few skin temperatures. Any factor that might influence general body condition, such as excessive reduction of diet, might logically be presumed to affect the arterial distribution of the blood, and hence skin temperature and heat-loss. Studies of rectal and skin temperatures were, therefore, included. The importance of studying the metabolism and the physiological activities at several nutritive planes led to observations during periods of maintenance, during prolonged submaintenance, and during the fattening period. Thus we have studied not only the influence of submaintenance rations, but likewise excess food, upon the several physiological factors.

No study involving pronounced alterations in diet is complete unless it contributes some evidence on the influence, if any, of such changes in rations upon the digestibility of the various nutrients, and particularly with regard to the nitrogen balance in the body. To this end, special metabolism stalls were constructed, and with certain of our animals complete nitrogen-balance experiments and continuous digestion experiments were carried out throughout the entire cycle of feeding.

## Economic Problems.

Any contribution to the physiology of maintaining an animal with least cost, physically uninjured and in condition to store fat and protein when abundant feed is available, has a profound economic significance. The cost of fattening an animal under ordinary nutritive conditions has been repeatedly studied, not only grossly by studying the relationship between weight of feed and gains in weight, but there has been a considerable amount of gasometric and calorimetric research on this problem. The possibilities of starting with a reduced body-weight, i. e., depots of body-fat in part depleted, and with the capacity to store fat possibly stimulated or increased by previous undernutrition, have not heretofore received calorimetric or gasometric investigation. Is there with previously undernourished animals a special stimulus to fill up reserves and store fat on the resumption of full feeding? The relationship between feed-supply, cost of material, and lower nutritive state of the animal, the remoteness of possible grazing lands, and particularly the fluctuating nature of the beef market, all are so interwoven that the animal husbandman can not afford to disregard any factor that may be shown to influence profoundly the nutritive condition and its effect on subsequent gains in weight of animals.

## PREVIOUS INVESTIGATIONS ON UNDERNUTRITION OF ANIMAL LIFE.

In this connection we, arbitrarily perhaps, leave out of consideration laboratory animals, such as rats, guinea-pigs, rabbits, and dogs, and deal primarily with the larger domestic animals, properly including man, for the purpose of this classification. Two subdivisions of the subject may be introduced: first, undernutrition as it deals with immature animals where the problem not only of body-fat and flesh maintenance enters, but specifically where the skeletal growth is an important factor; second, the influence of undernutrition on adult animals. On the subject of underfeeding during growth, the literature is practically limited to the most interesting experiments of H. J. Waters.[a] Indeed, Waters's observations were almost exclusively confined to growing animals and by control feeding he was able to hold immature animals at constant weight for long periods of time and measure the accompanying skeletal growth, although the body-weight did not change. Here we have a striking illustration of the capacity to grow and the drive on the part of the animal to complete its growth, even with deficient material. The research of Waters and its correlated studies have been extensively discussed in several bulletins from the Missouri Agricultural Experiment Station.[b] In our own problems this particular phase of the work did not play an important rôle, but nevertheless the influence of Waters's work upon our own investigations can hardly be adequately estimated. With adult animals, most of the information we have with regard to the matter of undernutrition deals with normal conditions of want (such as scanty pasturage), and the experience of herds during famines, crop damage, and excessive droughts. Almost no information is at hand with regard to the influence upon the animal of forced undernutrition, under controlled conditions such as stall feeding with minimum feed. Very little of this work has been done, for the simple reason that the whole trend of animal feeding is either to fatten all the time and as continuously as possible, or to feed rather liberally for maintenance. It is, however, of historic interest that one of the earliest contributions on this subject was by Sanborn,[c] of the New Hampshire Experiment Station, who reported in 1879: "It is worthy of note that I find the amount of hay required to maintain a thousand-pound steer without growth or loss of weight is less than that reported by German experimenters."

Physiologically, our previous evidence with regard to the influence of undernutrition in animals was drawn, singularly enough, chiefly from observations upon men, for usually the situation is quite the reverse and observations on men *follow* preliminary observations on animals. In this particular problem, however, the largest amount of data on undernutrition has been accumulated on men in researches such as those already cited from German laboratories

[a] Waters (Expt. Sta. Univ. Missouri), "The capacity of animals to grow under adverse conditions," Proceedings 29th Annual Meeting Society for Promotion of Agricultural Science, Washington, D. C., 1908, p. 71; also Waters (Expt. Sta. Univ. Missouri), "The influence of nutrition upon the animal form," Proceedings 30th Annual Meeting Society for Promotion of Agricultural Science, Portland, Oregon, 1909, p. 70.

[b] Trowbridge, Moulton, and Haigh, Univ. Missouri Agric. Expt. Sta., Bull. 18, 1915; *ibid.*, Bull. 28, 1918; *ibid.*, Bull. 30, 1919; *ibid.*, Bull. 43, 1921.

[c] Sanborn, Report Trustees New Hampshire Expt. Sta., 1879; also cited by Haecker, Univ. Minn. Agric. Expt. Sta., Bull. 79, 1903, p. 89.

and the study of the Nutrition Laboratory with regard to the college students at the International Y. M. C. A. College in Springfield, Massachusetts.[a]

Finally, there are the great economic national experiments, forced upon large communities, such as those in Austria and Germany, to say nothing of conditions in other countries, where great food shortage was experienced. In these instances volumes have been written (mostly by merely casual observers) with regard to the influence of undernutrition upon the public health, mental and physical activity, death-rate, fertility, and economic efficiency. Much of this information, unfortunately, has not the strictest scientific value, for the factors are so interwoven that it is difficult to make a sharp differentiation showing the influence of any one factor, such as undernutrition.

On men the findings are scientifically very extensive. Thus, experiments made both in German and American laboratories indicate that profound dietetic reductions can be made without seriously affecting the capacity to live and without impairment of mental powers. Clearly it is not, however, an optimum condition, although perfect and rapid resumption of the earlier nutritive state is immediately achieved on the resumption of full feeding. With wild animals under normal conditions of life, where food is at times very scanty, mature animals (and indeed immature animals) undergo great privations and periods of want and undernutrition without permanent detriment to the race as a whole. The weaklings undoubtedly are killed off and it may be argued that this very process of want, famine, and pest may of itself contribute toward strengthening the strain of any specific group of animals.

On the basis, therefore, of the evidence thus far at hand, it would appear safe to conclude that short periods of fasting or considerably prolonged periods of undernutrition do not result in either pronounced distress or permanent impairment of faculty, with either man or large animals, and thus, having first established the feasibility of such an experimental procedure upon men, our proposed study of the influence of reduced rations upon the vital activities of *large animals* appeared legitimate and feasible and without any danger of involving distressing complications, such as pain or permanent, irreparable damage to the animals.

[a] Benedict, Miles, Roth, and Smith, Carnegie Inst. Wash. Pub. No. 280, 1919.

# EXPERIMENTAL PLAN AND TECHNIQUE.

From the general trend of the discussion thus far, it is clear that our main object was to study the influence of undernutrition upon the general life-processes and welfare of these large animals. No one measurement with which we are familiar is such a good index of the general level of vital activities as is the direct or indirect heat measurement, and consequently such measurements were an essential feature of our study. Accompanying these, there would naturally be made the usual observations with regard to amounts of feed, digestibility, nitrogen excretion, general physical and bodily measurements, pulse-rate, body-temperature, and various other measurements. Our plan, however, centered wholly about the possibility of measuring by some means the heat-production of beef animals at different nutritive planes. All other observations were, at the beginning of the research at least, considered wholly secondary in importance.

## SELECTION OF ANIMALS.

In studying the effects of curtailed rations upon steers, we profited by the experience of the Nutrition Laboratory in studying undernutrition in man, in that at the outset it was recognized that the problem was too large and of too fundamental importance to jeopardize the research by confining our study to one or even two animals. Experiments with drastic ration curtailment were lacking. Experienced husbandmen predicted dire results, if not indeed death of the animals, and hence our first year's plan involved a study of 12 adult animals, of which 3, designated as Group I, were to be kept as a control, subject to all the experimental conditions of the others, but with sufficient feed to maintain the initial body-weight. The other 9 animals, after a month of approximate maintenance feeding, were divided into two groups, Group II of 5 and Group III of 4 animals, respectively, and subjected to a drastic ration curtailment.

With each group, containing not less than 3 animals, we felt well provided for contingencies or any untoward accidents, such as disease, incapacity, or, indeed, the death of any one or two animals of a group. At this point it is a great satisfaction to record that all 12 steers were without difficulty ultimately fattened for market and slaughtered. This is largely due to the extraordinary care and conscientious attention given them by Mr. Albert D. Littlehale.

After the first year's experience, in which we may anticipate our discussion by stating that the general picture of the physiology of animals on reduced ration was presented similarly by each of the 9 animals subjected to ration curtailment, we felt safe in confining our next series of experiments to steers A and B, making up Group IV. These 2, as the first 9, were subjected to drastic ration curtailment for several months, subsequently fattened and slaughtered, with no untoward incidents.

## CHARACTERISTICS OF STEERS 1 TO 12.

The selection of a sufficient number of steers to meet the requirements or objectives in view in this research was at best a difficult problem in this part of the country, where beef cattle are not very numerous. After some survey it was found impossible to secure 12 individuals, all of uniform age, breeding, and

conformation. The problem became somewhat more difficult, owing to the fact that it was imperative that the animals possess some degree of docility, so that they could be more easily handled in the respiration chamber and in making other daily observations, such as on pulse-rates, rectal temperatures, and live weights.

For the purpose of prolonged underfeeding, it was at first planned to use one control group and three subgroups representing various stages of submaintenance. It was assumed that each group should have at least 3 individuals in it so as to rule out in a measure the influence of individual variations as well as provide against accident, disease, or death. Twelve animals were finally secured which had at least one feature in common—they were all predominantly of Shorthorn blood, ranging from 40 or 50 per cent grade to 100 per cent or pure breeding. Unfortunately, uniformity in age and weight had to be sacrificed. In conformation, when judged as beef cattle, they presented somewhat less variation than in the purity of their blood lines. In fact, this variation was later easily balanced in the arrangement of the experimental groups. The greatest variation occurred in age. As classified by age, the animals fell into three distinct groups of 4 animals each, representing closely 3, 4, and 5 years. The individual characteristics of the animals, such as type (compared with recognized beef conformation, quality, and temperament), are factors on which practical stockmen base much of their judgment. The following descriptions serve in a measure to assign a relative value to each individual from the point of view of the stockman's experience. In fact, from both the scientific as well as the economic aspect, a fairly detailed characterization of the animals has served as a basis on which to establish their most useful place in the final arrangement of the experimental subgroups. For the present purpose this description is therefore taken up by groups as differentiated by age.

### Three-year-olds.

The three-year-olds (Nos. 2, 6, 7, 12) possessed on the whole the higher degree of Shorthorn breeding. No. 2 was pure bred and Nos. 6, 7, and 12 possessed about 75 per cent or more of Shorthorn blood. All 4 were roan in color. This group, though of good size, had evidently not attained full frame development, as will be seen by a comparison of their weights and measurements with those of the older groups (see Tables 10, 12, and 45, pp. 91, 94, and 174). From the stockman's point of view No. 2 excelled in conformation as a beef type, followed in order by Nos. 7, 6, and 12. This generalization is further explained in the following brief individual characterizations.

Steer No. 2 was an animal of fairly good size, weight, and proportions. He was fairly low set, compact in body, with fair depth and good width of chest. His chief faults lay in some lightness of hindquarters and some lack in depth of chest. In quality he was excellent, having smooth, dense bone, a soft, pliable skin, and a heavy coat of fine, glossy hair. His high degree of quality was further manifest in general smooothness of covering. In condition he was very good, as he carried a fair, even covering of natural flesh. This steer was a very good feeder type.

Steer No. 7 was an animal of good size, weight, and proportions. He was of slightly larger frame development and proportionately greater in weight than No. 2. He was of a similar beef conformation as No. 2, with somewhat greater

depth and width of chest. In quality he was somewhat inferior, as indicated by less fineness of bone and hair and less pliability of skin, and he was decidedly plainer and coarser in head than the former. In condition he was also slightly inferior by contrast, as he carried less natural flesh, though he was evenly covered and smooth. This steer was a good feeder type.

Steer No. 6 was of fair size and weight. In conformation he was inferior to both Nos. 2 and 7, as he had greater height and less body depth and width in proportion to his length; in other words, he was somewhat "leggy" and lacked compactness. In quality he was fair, possessing a fine, glossy coat of hair, a soft, pliable skin, and fine bone of fair density. In condition he was inferior to Nos. 2 and 7, lacking in covering of flesh. This steer was only fair as a feeder type.

Steer No. 12 was the smallest of the lot, both in weight and development of frame. In conformation he had some very pronounced faults as a beef type. He was decidedly too "leggy" and lacking in width throughout, the latter characteristic being very pronounced even in the head. In quality he was only fair, his coat being somewhat rough and his skin adhering too closely. In condition he was also deficient, as he carried only a thin covering of flesh. This steer was a poor feeder type.

### Four-year-olds.

The four-year-olds (Nos. 3, 4, 8, 11) were somewhat less uniform in breeding than the younger group. Nos. 3 and 4 were about 50 per cent Shorthorn, although their cherry-red color, the set of the horns, and conformation indicated some Devon blood, which is not uncommon in the State of New Hampshire. Nos. 8 and 11, though showing some Shorthorn evidence in color and conformation, seemed of more mixed breeding, and it is probable that they had less than 50 per cent Shorthorn. No. 8 was a dull red, tending to roan, with some white patches, and No. 11 was a light red with white patches.

From the measurements it will be observed that this group also had not attained their complete development of frame, as they were approximately midway between the three-year and five-year group in size of trunk-length, in height, and in chest circumference, the average measurements and weights by groups being as follows:

| | Trunk-length. | Height. | Chest circumference. | Average weight in pounds. |
|---|---|---|---|---|
| | *cm.* | *cm.* | *cm.* | |
| Three-year-olds... | 143.4 | 121.9 | 179.9 | 975 |
| Four-year-olds... | 150.0 | 125.3 | 186.5 | 1,117 |
| Five-year-olds.... | 161.9 | 131.9 | 198.1 | 1,302 |

Steer No. 3 was of good size, fairly low set, with good depth of body, but lacking in width of body. In other words, he lacked what is in practical terms spoken of as "spring of rib." Except for this fault, he would have been a good feeder type, since he possessed that other common index of a good feeder, "quality," in a high degree, as indicated by dense, clean bone, soft hair, and

a pliable, elastic skin. He was evenly fleshed and would be called a fair feeder type.

Steer No. 4 was in all respects a duplicate of No. 3 except that he had the additional merit of greater body-width or spring of rib, making him on the whole a good feeder type.

Steer No. 8 was on the whole the runt of this lot in size and weight. He was especially lacking in depth of chest and in development of the hind quarters, which were rather narrow, and he was cut up in the flanks. On the other hand, he had good spring of rib and handling of his hair and skin suggested fair quality, but on the whole he would be considered an indifferent feeder type.

Steer No. 11 compared very favorably with No. 4 as a beef animal. He was of about the same size, weight, and proportions. Except for a tendency to lightness of hind quarters, he would have been the best feeder steer of this lot, though he easily stood second to No. 4.

### Five-year-olds.

The five-year-old group (Nos. 1, 5, 9, 10) were, as already indicated, considerably larger in size of frame and in weight than either of the other two groups. In fact, they would be generally referred to as oxen, having very probably been used considerably to yoke. These animals had undoubtedly attained complete development of frame. Collectively they were not of as good beef conformation as either of the other groups, and their general appearance suggested a more mixed breeding, with Shorthorn characteristics somewhat more clearly evident than any other blood lines. In live weight the group was very uniform, the average being close to 1,300 pounds, the range representing less than 50 pounds difference.

Steer No. 5 was the best of this group. Although of slightly less frame development than the three other individuals, he was the heavier, being low set, with materially greater width of body and well-developed hind quarters. He was on the whole a good beef type, comparing favorably with Nos. 2, 7, 4, and 11 in conformation, quality, and condition of flesh.

Nos. 1, 9, and 10 were coarse-boned, rangy individuals, of great frame dimensions. No. 10 was somewhat the better beef type of the three, as he showed less tendency to coarseness and was better developed in hind quarters. He was only an indifferent beef type, showing, for his age, neither decidedly good nor inferior characteristics. No. 1 was the coarsest animal of the 12. He was large of frame with rather long legs and was lacking in depth of body. He was heavy, coarse-boned, with prominent hips, and very deficient in development of hind quarters. On the whole, he was an inferior beef feeder type. No. 9 also showed considerable coarseness of bone. He had good depth of body, but was especially lacking in width of body and in development of hind quarters. He was of exceedingly inferior beef type.

## CHARACTERISTICS OF STEERS A AND B.

The primary object of the second year's work was to conduct a nitrogen-balance experiment under conditions of feeding as nearly identical as possible with those under which the 9 submaintenance steers had been kept the year before. It was decided, therefore, that 2 steers would be purchased for this purpose, since the details involved in prolonged metabolism experiments

would not permit the use of a greater number. In the selection of animals, due consideration was given to the essential fact that they should correspond closely in type and breeding to the steers used in the previous year's work. Owing to the limited number, however, it was decided to use only animals of mature growth, reserving the study of metabolism during growth for a future period.

The two animals finally selected met in a general way the essential requirements of this work. Both were predominantly of Shorthorn type as regards color, conformation, and size of frame, possessing probably between 50 and 75 per cent of that blood line. Steer A was apparently of a somewhat higher grade than steer B, since the proportions of his measurements were better; in fact, the black color-markings of muzzle, horns, and hoofs of steer B suggested a trace of Holstein. Both were basically red in color, with considerable white in the form of large patches, principally on the legs and underline.

In weight and size of measurements, steers A and B were equal to the older group used previously (Nos. 1, 5, 9, and 10), though at least a year younger in age. In conformation, judged as beef types, they compared very favorably with the other 12 animals.

Steer A, in fact, was on the whole the equal of, if not superior to, any of them, since he had no particular defect in conformation. He was low-set, with excellent depth and width of chest. This, together with a broad back, short and closely knit body, and well-formed hind quarters, combined to make him an excellent beef type. In quality, steer A was fairly good, though not quite equal to Nos. 2, 3, 4, and 11, but certainly superior to Nos. 1, 9, and 10 of the older lot. He was fairly heavy-boned, though not coarse, and while his skin was rather thick, it was mellow, pliable, and covered with a thick coat of soft hair.

Steer B was not quite equal to steer A in conformation, though resembling the latter so closely that they were generally considered a well-matched pair. Steer B was somewhat lighter in weight than steer A. He had slightly more depth but considerably less width of chest and body, and he was not quite so well formed in the hind quarters. In quality he was about equal to the former. He was on the whole only fair as a beef type and as such compared with Nos. 3, 6, 8, and 10, everything considered.

## GROUPING OF ANIMALS.

In making up our experimental groups, very careful consideration was given to the individual traits and characteristics of each animal. The basic plan for the first year's work was to use three groups, one of the groups to be fed on maintenance as control, one on 33⅓ per cent below maintenance, and one on 50 per cent below. Numerically, the control group needed the smallest representation, since considerable data on full maintenance were already available. Furthermore, since the critical factor or objective was the effect of prolonged undernutrition, it was recognized that the larger the number on which this vital question could be tested the more reliable would be the data. Hence, in the final arrangement 3 steers were selected for control on full maintenance, 5 for a feed-level representing only 50 per cent of their tested normal maintenance requirements, and 4 for a feed-level representing

66⅔ per cent of their tested normal maintenance requirements. The latter feed-level was, in fact, established only as a safety provision at the beginning, and after 7 weeks, when it was found that they were all in apparently excellent health, though naturally losing in flesh, this group was reduced to nearly 40 per cent of the original maintenance requirements.

### Control Group (Maintenance), Group I.

In order to forestall any possible criticism which might arise by selecting the best animals for submaintenance, on grounds that they would perhaps be more resistant and would recuperate better on refeeding later, the three best animals were selected for the control group. From previous descriptions it will be seen that the logical selection was Nos. 2, 4, and 5, representing respectively the three-, four-, and five-year-old groups.

### One-half Maintenance, Group II.

Since the effect of a 50 per cent maintenance ration for a period contemplated to run close to 150 days was *a priori* an unknown factor, it was decided that Group II, being the important group, should be represented in largest number and by the best of the remaining individuals from each separate age-group. The selection, therefore, included No. 7 representing the three-year-old class, Nos. 3 and 11 representing the four-year-old class, and Nos. 1 and 10 representing the five-year-old or adult class.

### Two-thirds Maintenance and Two-fifths Maintenance, Group III.

The four steers left for this group were the inferior animals of the herd. Nos. 6 and 12 were easily the poorest individuals of the three-year class, No. 8 of the four-year class, and No. 9 of the five-year class. However, it was assumed at first that, being physically inferior, they might not stand any serious feed curtailment so well, an error of judgment which was later corrected by reducing them even more severely than the half-maintenance group, with no noticeably serious effects on their general health.

### Animals for Digestion and Nitrogen-balance Trials, Group IV.

A year later the two adult steers, A and B, were used to repeat certain of the ration-reduction tests, with the added important factor of nitrogen-balance and digestion experiments. Since these animals were to spend practically their entire time in metabolism stalls, they were selected for temperament as well as age, weight, and general conformation.

## PLAN OF FEEDING, RATION CURTAILMENT, AND SUBSEQUENT FATTENING.

Naturally, rather precise plans for feeding these animals preceded their purchase, and as the animals in Group IV represent a somewhat special problem, we will first consider in detail the feeding plans for Groups I, II, and III, i. e., the animals used in the first year's work, and subsequently the special feeding features attending the experiments with steers A and B will be detailed.

### Feeding and Ration Curtailments of Groups I, II, and III.

During the preliminary period an attempt was made to approximate as nearly as possible the probable maintenance requirements of each individual. Assuming that the maintenance requirements given by Armsby[a] would meet

[a] Armsby, U. S. Dept. Agric., Bureau Animal Industry, Bull. 459, 1916, p. 14.

the needs of these individual animals, a ration was first calculated on that basis and on the further assumption that the digestibility of the hay used[a] (hay alone forming the ration) would be approximately similar to that of redtop, a grass which is relatively high in true protein and yields a high percentage of energy. But the final amount accepted as maintenance was based on its influence on the live-weight variations of each individual.

After the animals were placed in their permanent stalls, the hay, given in two daily feeds, was weighed out to them at the time of feeding, and all refuse or left-over hay was carefully brushed up and weighed. Feeding was begun on November 27, 1918, on fairly liberal quantities at first. The oldest steers (five-year-olds) were fed 30 pounds daily and the other two sets (four-year-olds and three-year-olds) 24 and 22 pounds, respectively. This amounted to about 20.7 pounds of dry matter per 1,000 pounds live weight in the first lot and to 21.6 pounds for the two younger lots, allowing a little excess for growth in the latter. It was soon found that all animals increased in weight on their respective amounts of hay, though the increase was no doubt due in part to a greater fill and high water consumption.[b] Gradual reductions were then made to determine the least amount on which they would hold their weight with the barn conditions under which they were kept. Based on variations in weight resulting from quantitative variations in feeding, it was found that about 16 pounds of dry matter per 1,000 pounds weight furnished by the hay used would hold their weight equilibrium. There were, of course, some slight variations from this between individuals.

For the sake of convenience in weighing feed and also to avoid errors, no attempt was made to meet exactly the demands of each individual animal as based on their actual live weights or physiological differences. A uniform weight representing the average weight of each age-class was accepted as a standard for each group and the amount fed was calculated on that standard. The four younger steers were fed on a 1,000-pound standard, though they varied between 900 and 1,050 pounds. The four-year-olds, which varied between 1,100 and 1,175 pounds, were fed on a 1,150-pound basis, and the older lot, which varied between 1,275 and 1,325 pounds, were classed and fed on a 1,300-pound basis. To have scaled their feed in ounces or grams to meet exactly the standard maintenance requirements based on actual weight would obviously have involved such minute exactions in the daily weighings as to increase the chance for error where feed was not weighed out into daily rations for long periods in advance.

### METHOD OF FEEDING AND WATERING.

During the maintenance and submaintenance periods (November 27, 1918, to May 12, 1919, inclusive) only native hay was used for feed. The hay was not chopped or in any way specially prepared. Throughout the experimental period it was given in two daily feeds (at $6^h\ 30^m$ a. m. and $4^h\ 30^m$ p. m.), and the amount given per feed was weighed out at the time of feeding.

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[a] The actual analysis (one sample only) of the hay used is given in table 2, p. 36.

[b] To reduce error in the great variations that may occur from one day to another in live weight due to unequal feed and water consumption or to unequal elimination of waste, the steers during the first year's work were weighed daily about 6 a. m., i. e., before feeding and watering. From these daily weights averages of a week could be secured, representing with a fair degree of accuracy the live weight coincident with the respiration experiments.

*Weighing feed.*—In order to avoid errors of variation in weight, large 2-bushel baskets were used, in which the hay allowance was weighed, the baskets all being counterbalanced to the same weight with lead, and the feed allowance was made on a basis of the nearest half pound required.

*Feed refused* was weighed daily and deducted from the amount given in calculating feed consumed. As a matter of fact, practically no feed was refused, especially in the submaintenance periods, except now and then a few sticks and extraneous indigestible matter, such as tough, fibrous weeds which chanced to be in the hay.

*Water* was given once a day only (10 to 11 a. m.) during submaintenance feeding. In fact, it was found that, especially during cold weather, the steers would not take water more frequently, and several individuals would take it only every second day. The water was given in heavy, galvanized-iron pails which held approximately 20 pounds when full, and the amount refused was estimated to the nearest quarter part of a pailful. Thus a fairly close estimate was obtained of the total water consumption.

### PRELIMINARY MAINTENANCE FEEDING PERIOD.

Nearly a month previous to the beginning of the submaintenance feeding a preliminary feeding period on the hay to be used later was begun, first, to adjust the steers to the character of the feed, and, second, to determine the amount necessary to maintain their live weight without gain or loss. This method for determining the maintenance requirements seemed preferable to accepting the conventional Wolff-Lehmann or Armsby standards, since the digestibility factor of the hay was unknown. After 25 days' trial, based on daily weight variations of the animals, a supposed maintenance requirement was estimated for each individual.

This preliminary or maintenance period began with a week's feeding (November 27 to December 2), during which the approximate maintenance requirement was more or less closely determined for each steer. After the maintenance requirements had thus supposedly been fairly closely determined for each individual, the steers were fed at this nutritive level from December 2 to December 22, on which date the feed reductions were made.

### SUBMAINTENANCE RATION PERIODS.

After the preliminary period of maintenance, the two groups selected for prolonged undernutrition were reduced in feed about one-half and one-third respectively, from their maintenance requirements. The curtailment was made suddenly, as there seemed to be no particular advantage in resorting to a slow adjustment on a downward scale. The group that was reduced by only one-third of their maintenance requirements was eventually given even a more severe rationing, since there was every indication that they would not suffer seriously, except in loss of flesh, from such treatment. The time covered under the various conditions of feeding was as follows:

Group I, 3 steers, control (maintenance), December 2, 1918, to May 12, 1919, inclusive.

Group II, 5 steers, submaintenance (50 per cent), December 22, 1918, to May 5, 1919, inclusive.

Group III, 4 steers, { submaintenance (66 per cent), December 22, 1918, to February 7, 1919, inclusive.
submaintenance (40 per cent), February 8, 1919, to May 5, 1919, inclusive.

From May 6 to May 12, inclusive, 1919, Groups II and III were again fed the original maintenance supply of hay, partly to determine the relative difference in weight due to fill, but also to determine the energy metabolism on original maintenance after undernutrition.

### REFEEDING AFTER SUBMAINTENANCE.

After submaintenance had been brought to a close, May 5, 1919, a plan of procedure for refeeding was agreed on in conference with Professor Henry Prentiss Armsby, who kindly consented to come to Durham to inspect the nature and progress of the experiment. Since the winter's operation represented a rather severe test of the possibilities in the practice of food economy, it was the consensus of opinion that the main problem involved in refeeding was a comparison of the economy and rate of regain between the steers which had been wintered on full maintenance and those which had been wintered on one-half that amount or less.

A number of points were involved in the question whether the feed saved with less than a maintenance ration during the winter season is actual economy, since it means that the live weight lost by submaintenance must eventually be replaced by less feed than the feed saved on submaintenance. In other words, there were several angles to the question of the economy with which the weight lost by subfeeding could be regained. For example, could this loss of weight be recovered by original maintenance alone, and if so, how rapidly? Could it be regained by the original maintenance plus the feed saved? Could it be more economically regained on pasture, in which case submaintenance would constitute a real saving? Would animals which had been wintered on submaintenance respond more quickly and efficiently to the use of grain for fattening? Would the submaintenance animals make the more economical gains on a wide ration, i. e., protein-poor, or a narrow, protein-rich ration?

*Regain on original maintenance ration.*—Digestive efficiency is recognized as a merely relative question, since the coefficient for the same feed varies materially between different classes of farm live stock, such as horses, cattle, and pigs, it varies somewhat between individual animals of the same types and breeds adapted to the same general purpose, and it is even known to be somewhat variable with the same individual animal at different times under different conditions of feeding and treatment. In how far the resumption of the original hay ration would affect the regain in weight was tested in that all animals were fed on original maintenance (hay) for one week, although it was realized that any increase in weight would represent largely a change in fill and water, since very little tissue increment could be expected in so short a time. However, to test this problem more thoroughly, one mature animal (No. 10) of the submaintenance group was selected to determine the rate of recovery of flesh to the original weight when fed a normal maintenance ration (based on original live weight) of hay only; in other words, on double the weight of hay on which he had been carried through the winter, and on which he had lost 22 per cent of his gross live weight.

*Regain on pasture.*—The question of regain on pasture, as a sequel to the submaintenance wintering of beef cattle, is a problem of primary and fundamental economic importance where pastures are plentiful, crop land scarce, and where winters are relatively very long and costly from a feeder's point

of view. In fact, it is a practice not uncommon in sections of the country where little or no grain is produced, such as the range areas, and even in New England, to carry cattle through the winter on a relatively low nutritive plane, in the belief that good pasture offsets any possible loss in weight or growth of animals so treated during the preceding winter. It was therefore deemed advisable to use 3 animals to check up this question. One of the animals (No. 2) selected for this purpose was of the younger group, about 3 years of age at the time when put on pasture (May 20). During the winter period No. 2 had been on full maintenance. He was turned out into a large pasture with 7 Hereford steers of about the same age. No special data were gathered from him, as the pasture was too remote to permit getting daily or even weekly records of weights, etc. He remained on pasture until slaughtered. The other two steers (Nos. 6 and 9) also used for refeeding on pasture, were selected as fairly representative examples of average beef steers. Both had been carried on submaintenance rations during the winter. They were turned into a pasture adjoining the barn, so that daily records of weight and pulse could be secured. Steers 6 and 9 had to be taken off pasture during the last 6 days before slaughter, as cold weather suddenly set in. No. 6 was therefore given a high-protein feed and No. 9 a low-protein feed during these last 6 days (October 29 to November 3). In selecting these 3 animals to test out the regain on pasture, it was decided to make the test under as severe a comparison as possible. In other words, the best individual (No. 2) was selected as a control, so that if the submaintenance steers should show a higher relative regain than the controls there could be no criticism on grounds favoring the regains in the submaintenance animals in the comparison by selecting an inferior control.

*Regain on heavy grain rations.*—The feeding of heavy grain rations as practiced under normal conditions is a notably uneconomic procedure if taken purely from the point of view of digestive efficiency. It is commonly accepted[a] that the more an animal consumes the greater becomes the percentage of food that passes through the animal undigested or less thoroughly digested. In fact, it has been demonstrated by the live-stock feeders of the corn belt that fattening cattle for market under normal conditions would be a losing venture, except for the gains made by hogs which follow the cattle in the feed lot, picking up practically all the grain which has passed through the cattle incompletely digested. Since heavy grain feeding is the standard method of fattening cattle, its effects on the submaintenance animals were considered as particularly worthy of note. The remaining 8 steers were therefore put on heavy grain rations to contribute to the following problems:

1. The capacity of animals wintered on submaintenance rations to consume and to assimilate feed.
2. The thoroughness of food assimilation by such animals (subnormal in weight), as indicated by increase in weight and its ratio to the feed consumed.
3. The relative effect on fattening of rations high in protein and rations low in protein in animals of approximately mature growth.
4. The relative effect on fattening of similar rations in animals not of mature growth.
5. The amount of feed necessary to regain the loss in weight below normal flesh due to a long-continued, submaintenance ration.

[a] Henry and Morrison, Feeds and feeding, Madison, Wisconsin, 1916, 16th ed., p. 50.

These animals were therefore divided into two main groups of 4 animals each. One group was fed a ration high in protein, and the other group a ration low in protein. In making the assignments of the steers into the two respective groups several factors were given consideration. (1) None of the older steers (i. e., 5 years old or over) were put into the high-protein group, these animals being of mature development. Hence any unnecessary substitution of protein-poor feed by feed high in protein would, under normal conditions, be economically unsound. (2) All animals in the high-protein group were therefore such as had not entirely completed growth. (3) Both mature and immature animals were represented in the low-protein group. (4) The two groups, judged by their probable capacity (i. e., the usually accepted indications of good feeder steers) to digest and assimilate feed, should be balanced as nearly as possible, regardless of age.

*High-protein group.*—The steers chosen for this group were Nos. 3, 4, 8, and 12. Nos. 3, 4, and 8 were 4 years old and No. 12 was approximately 1 year younger. No. 4 had been carried on full maintenance all winter. No. 3 had been carried on somewhat less than one-half maintenance throughout the whole winter period and Nos. 8 and 12 had been on 60 per cent maintenance up to February 8, on which date they were cut to about 40 per cent maintenance, based on their own original weight. This group was fed on high-protein meal mixture (with hay as roughage) from May 13 until slaughtered. This meal mixture was made up in equal parts by weight of linseed meal (old process), cottonseed meal, and wheat bran.

*Low-protein group.*—The steers chosen for this group were Nos. 1, 5, 7, and 11. Nos. 1 and 5 were of full growth, being over 5 years of age. No. 1 had been on somewhat less than 50 per cent maintenance all winter and No. 5 had served as control for the same period. No. 11, one of the intermediate-sized animals of similar age as Nos. 3, 4, and 8 (high protein), had been carried on somewhat less than one-half maintenance. No. 7, one of the younger steers, being of a similar age as Nos. 2 and 6 (pasture) and No. 12 (high protein), also had been on somewhat less than one-half maintenance during the whole winter. This group was fed on a low-protein meal mixture (with hay as roughage) from May 13 until slaughtered. This grain mixture was made up of 1 part of wheat bran and 2 parts of whole dent-corn meal, coarsely ground.

*Regain on original hay maintenance ration.*—Steer No. 10 was selected for this purpose. From May 13 to July 7 this animal was given the original hay maintenance ration. From July 8 to November 3 he was in the high-protein group and he was fed under the same conditions as regards the nature of the feed given.

### Feeding, Ration Curtailment, and Fattening of Steers A and B.

These two animals were used the second year to verify certain points raised by the first year's work, and particularly to serve as subjects of numerous digestion experiments and nitrogen metabolism experiments. Since the latter was to be one of the most important phases of the year's work, the animals were retained in metabolism stalls practically the entire time of observation. Thus, they were much restricted as to activity as compared with steers 1 to 12.

## PLAN OF FEEDING.

In temperament and general behavior both steers A and B were somewhat more placid (i. e., less nervous) than any of the other 12 steers. They were exceedingly tractable and easy to manage, which was a great advantage in the metabolism work, since they adjusted themselves very readily to the rather irksome conditions of close confinement, lack of exercise, and the inconvenience of the harness and urine funnels. They were taken off pasture on the day when they were purchased, November 1, 1919, having been on pasture all summer and fall. They were then kept in a barn, where they received hay only, until they arrived at the experiment station on November 14. Up to December 1 they were kept in a barn, where they were weighed daily and fed all the hay that they would readily consume. On December 1 the scales were moved to the college dairy barn, where the metabolism stalls were being erected, and weighing had to be discontinued until December 27, when the metabolism stalls were ready for use. From December 15 to December 27 a preliminary feeding period was conducted, during which they were fed an approximate maintenance ration (computed on the basis of live weight and of the previous year's work), so that they would be adjusted to this feed-level when they entered the metabolism stalls. This was a rather short period in which to determine this point accurately, but on the basis of observations of weight-changes of steers 1 to 12 it was assumed that the 26 pounds of hay which were first given would supply more than the necessary amount for weight maintenance, so that during the preliminary feeding the steers were finally brought down to 24 pounds per head daily and during the period of closer confinement in the metabolism stalls their maintenance ration was finally approximated at 9,090 grams per day.

TABLE 1.—*Hay eaten by steers A and B during preliminary feeding period.*

| Date. | Hay eaten by— | | Date. | Hay eaten by— | |
|---|---|---|---|---|---|
| | Steer A. | Steer B. | | Steer A. | Steer B. |
| 1919 | *kg.* | *kg.* | 1919 | *kg.* | *kg.* |
| Dec. 15 | 13.6 | 12.7 | Dec. 21 | 9.8 | 9.3 |
| 16 | 13.6 | 12.7 | 22 | 10.4 | 9.3 |
| 17 | 10.9 | 10.9 | 23 | 10.9 | 10.0 |
| 18 | 12.2 | 10.9 | 24 | 9.8 | 8.0 |
| 19 | 12.8 | 11.8 | 25 | 10.9 | 10.0 |
| 20 | 13.6 | 10.9 | 26 | 10.2 | 9.4 |

During the preliminary feeding period, December 15 to 27, the hay used was of a variety commonly known as "mixed hay," containing some clover, timothy, and redtop mixed with other native grasses. This was not the same hay as that used subsequently during all the digestion experiments and it was not analyzed. The cut from the total that they would consume to the calculated maintenance (24 pounds or 10.9 kg.) was made gradually, as shown in Table 1. During the main feeding periods, i. e., the periods during which the digestion balance was made, the general conditions of feeding steers 1 to 12 were duplicated with steers A and B as nearly as practicable, as regards quan-

tity and quality of feed. Thus, the hay was purchased from the same farm as the hay used in the experiment with steers 1 to 12. Approximate maintenance or slightly less was fed for a short period, and then a sudden reduction was made to one-half that amount.

### Feeding during Balance Experiments.

Theoretically it would have been very desirable to have been able to establish the precise maintenance requirements in advance, on the basis of live weight as provided by the conventional standards, but it was recognized that this would be practically impossible[a] and that they could be determined only by the results of the experiment itself. The standard requirements were, therefore, used largely as a general guide, subject to necessary modifications in order to approximate closely to the actual needs.

During the first and the twelfth aliquoting periods (each aliquoting period including 14 days) such an approximated maintenance was fed. During maintenance and submaintenance both steers were given the same amount of feed as a matter of convenience, as well as to avoid complications, although they varied about 75 pounds (34 kg.) in weight, steer A being the heavier. They were actually given 9,090 grams each, which in the case of steer A amounted to only 75 per cent and with steer B to 80 per cent of standard requirements. During submaintenance each received just half that amount.

All the hay used during the digestion-balance experiment was cut in advance in a feed-cutter, a ton or more at a time, mixed and sampled for analysis, and immediately weighed into rations of equal weight, which were placed in bags and stored. In this operation of preparing rations in advance the same procedure was followed as given by Armsby.[b] Each bag contained a total daily ration, although it was given in two separate feeds, one in the morning and one in the evening. A fresh bag was always opened for the evening feed, when the animal was given approximately one-half of its contents, the remainder being fed the following morning, so that the exact total of each bag came within the same 24-hour period, corresponding to one 24-hour collection of feces and urine. During the maintenance and submaintenance periods, when hay only was used, the morning feed was given at 6 a. m. and the evening feed at $4^h\ 30^m$ p. m. When grain was added to the ration the morning grain ration was given at 6 a. m. and the hay at 7 a. m. In the evening the grain was fed at 4 p. m. and the hay at $4^h\ 45^m$ to 5 p. m. This gave the animals time to clean up the grain before the hay was put into the feed-box. This arrangement was found very satisfactory, since they cleaned up grain quite readily, but often took 2 or 3 hours and even more to eat their hay when on super-rations. When the animals were prepared for respiration experiments, two feeds were always withheld before the experiment, namely, the afternoon feed of the day preceding the experiment and the feed on the morning of the experiment. During the submaintenance stage the two withheld feeds were always made up, one being given as soon as the animal came out of the respiration chamber and the other as a noon feed on the following day. Feed refused was collected in tight cans

[a] It was found during the preliminary feeding periods of both steers A and B as with steers 1 to 12, that daily variations of 4 to 5 pounds of hay tended to fairly large variations in water intake, which apparently caused relatively large variations in fill, manifesting itself in proportionate variations of (artificial) live weights.

[b] Armsby and Fries, U. S. Dept. Agric., Bureau Animal Industry, Bull. 128, 1911, p. 201.

and the total weighed at the end of each aliquoting period, although, with the exception of period 1, practically no feed was refused.

### Details of Procedure in Digestion Experiments.

The daily routine of work was so arranged as to avoid as much as possible too great complications in detail, both as a matter of saving time and to insure accuracy in its performance. Every operation was, therefore, systematized as much as possible on an exact time schedule. A day in metabolism operations, therefore, included the 24-hour period beginning and ending at 2 p. m. This particular hour offered many advantages in dividing the daily periods: (1) the animals would drink more regularly at 2 p. m. than when watered in the morning, especially if watered early; (2) since the animals were weighed promptly at 2 p. m., the live weights were obtained at the end of the period, 24 hours after the last water intake (the water intake corresponding to a 24-hour collection of urine and feces was determined at the beginning of the corresponding period); (3) additional weighings were avoided; (4) it was more convenient to conduct respiration experiments during the morning, since the electrical power was interfered with less at that time (the animals were therefore deprived of their feed in the evening before an experiment, which caused less restlessness, since they were naturally less restless during the night) and every afternoon was left free to attend to the weighing of the animals and the collecting of aliquots of the visible excreta; (5) the main feature of this arrangement had as its objective a coordination in the weighings, respiration experiments, and intake of feed and water, with the weights of visible excreta during a stated daily or 24-hour period.

The following procedure was observed in weighing the animals and in the collection, weighing, and sampling of aliquots: (1) exactly at 2 p. m. the containers with feces and urine were removed and replaced by empty containers; (2) each steer was then weighed and watered while standing on the scale-platform, and reweighed before leaving the scale, after which he was again placed in the stall; (3) the urines were then weighed, and aliquots taken for preservation; (4) feces were then weighed, placed in a mixing tray, where they were thoroughly mixed, and aliquots were taken for preservation; (5) after this procedure all vessels were carefully washed, and placed aside to dry; (6) feed was given at 6 a. m. and $4^h\ 30^m$ p. m.

### Aliquoting Periods.

The question of the number of days necessary for obtaining representative aliquots of feces and urine was discussed with Professor Armsby, who proposed to us the following procedures.

A picture of the nitrogen balance (retained or lost by tissue), determined by difference between feed-nitrogen and nitrogen in visible excreta (including hair-growth), can be obtained either by analysis of samples representing all excreta or by samples representing broken periods, i. e., where collection periods alternate with intermediate periods in which the animal is gradually prepared for the collection period, when for some reason normal feeding is interrupted, as, for example, by starvation, change to different feed mixture, or change in quantity of feed.

Several options are therefore open for procedure as follows: (1) continuous daily collection, 7 to 14 days aliquoting, except for the days in the respiration

chamber; (2) alternating collection and preparation periods, 10 days weighing and aliquoting of excreta, 1-day respiration chamber and no aliquots, 10 to 17 days weighing of excreta only, but no aliquots.

The first of these options, i. e., a continuous measurement of the income and outgo, was accepted as preferable over the periodical measurement in which only 10 out of every 28 days would actually be analyzed. A device was made whereby both feces and urine could be collected in the chamber, and aliquot samples were collected without material break for practically the entire year.

### Refeeding Program.

Steers A and B were first turned on pasture, where they were kept without any additional feed from June 12 to October 15, 1920, when they were again placed in the metabolism stalls and fed on hay alone (amount not recorded) until October 22. After October 22 they were heavily grain-fed till slaughter, December 21, 1920. During this 8-weeks' fattening process steer A was fed a low-protein ration corresponding to that given steers 1, 5, 7, and 11, and steer B was given a high-protein corresponding to that given steers 3, 4, 8, and 12, the hay being the same and the grain mixtures being made up in the same proportions.

## HOUSING AND EXERCISE.

*Groups I, II, and III.*—Throughout the experimental feeding, the steers, with the exception of Nos. 2, 6, and 9, while on pasture, were kept in an ordinary well-protected stable, where they were tied by means of the common neck tie-chains which gave considerable liberty of movement. They obtained some exercise about once a week when taken to and from the respiration chamber, a distance of 300 meters each way, and up to the middle of April they were turned out daily into a large bare lot, fenced in with woven wire, where they were allowed to exercise for about an hour and a half. It was impossible to turn them out for exercise after the grass began to sprout, as they threatened to break down all fences to reach the grass.

*Group IV.*—These two animals, A and B, were confined the entire time to the metabolism stalls, save for the time of weighing and the occasional short trip through the basement of the barn to the respiration chamber.

## BARN ARRANGEMENTS.

For the first year's work, i. e., 1918–19, a section of one of the college sheep barns was remodeled for the use of steers 1 to 12. No heat was provided in the building, but as it was located in a small clearing of the college woods, it was very well protected from wind. The stalls were constructed in a row along the south side of the building, to get the advantage of sunlight through the numerous windows. Along the front of the stalls (which faced north), a solid partition was placed, so that during cold weather the temperature of the stable could be somewhat modified by keeping the doors and windows closed. Ordinary board partitions were constructed, reaching about half the length of the stall, to give the animals somewhat greater freedom of movement and permit better access to them. These partitions, built to a height of about 5 feet, were projected forward to meet the board wall along the front of the stalls, thus forming mangers in which hay was fed, individual removable boxes being provided for feeding grain. Drop doors in the front wall per-

mitted feeding and watering without going into the stalls or removing the animals. The water was given in large pails. The animals were held fast by means of common neck tie-chains, the ends of which were given about 2 feet of play up and down by means of a ring sliding on an iron rod, which was bolted to upright 4 by 4 inch posts. These posts, located at the usual place for stanchions, were set 20 inches apart, so as to give more freedom of movement for the animal. A rectangular bare lot, 50 by 150 feet, located directly at the rear of the building and fenced in with woven wire, served as an exercise yard.

### Metabolism Stalls and Appliances.

As the investigations with cattle after the first year's work involved digestion experiments, it became necessary to provide specially designed stalls by means of which the intake and outgo of nitrogen and dry matter could be determined with a considerable degree of accuracy. Furthermore, it was necessary that these stalls should be located where the temperature would not reach the freezing-point, as this would have made it impossible to secure representative samples or aliquots of the visible excreta. Suitable stalls were therefore erected in the basement of the dairy barn (see Fig. 1), which served as a temporary location until more permanent quarters were secured.

To determine the balance between income and outgo of nitrogen, it is necessary to make a careful collection of all the feces and urine. The appliance which has been most generally used for collecting the urine is the rubber funnel, attached to the male animal by means of a simple harness consisting of ropes or belts. The urine funnel is connected by means of a rubber hose to a suitable container for the urine, which is preferably located under the floor on which the animal stands.

The provision for satisfactory collection of the feces has, in a sense, offered more difficulty, there being a greater chance for loss by evaporation and by general wastage. A number of different methods for the collection of feces have been used, ranging from the employment of an attendant who is on duty continuously with a shovel to collect the excretions as they are voided, to the use of the more elaborate rubber or oil-silk excreta ducts which are directly attached to the animal. Probably the best arrangement to insure accuracy in collection of feces and to reduce personal attendance to a minimum is that used at the Institute of Animal Nutrition at State College, Pennsylvania. At about the center of the usual location for the manure gutter, a round opening is made through the floor (about 6 to 8 inches in diameter) through which a long rubber duct, attached to the rear of the animal, is projected into a suitable container under the floor on which the animal stands, this floor being raised about 4.5 feet above the floor-level of the room in which the stalls are located. The metal receptacles are fitted closely against the flooring underneath in order to reduce to a minimum the air-drafts and their desiccating effect on the feces. The proper utilization of such an appliance, however, requires a specially designed stall which will prevent the animal from making any very great shifts of position and thus avoid waste by keeping the animal, when standing, near the center of the opening, and which will yet allow of sufficient freedom to give the maximum amount of comfort possible under such restriction. For a more or less permanent investigation of this kind it is also desirable that the stalls allow a certain measure of adjustment to meet the

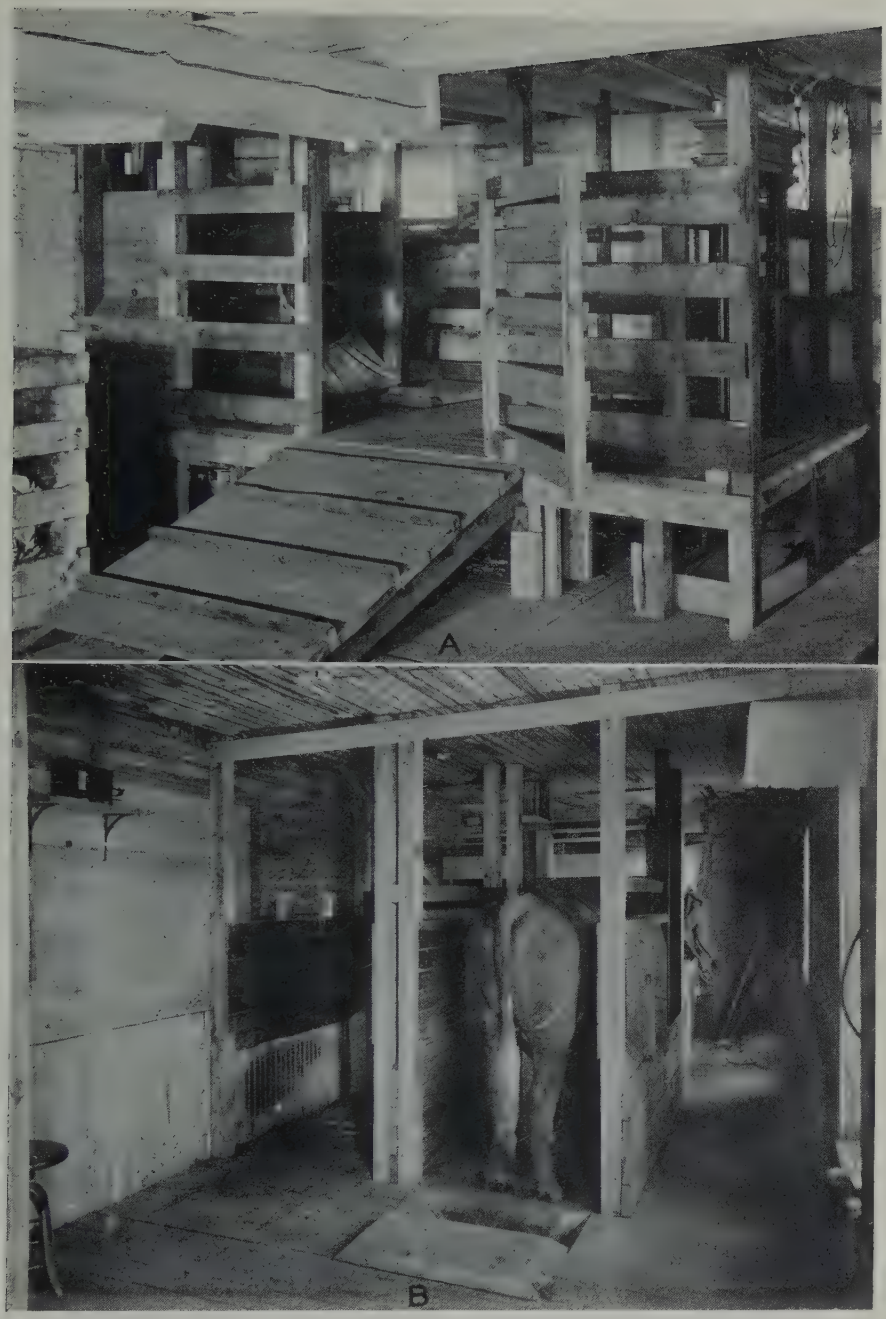


FIG. 1 (A).—Metabolism stalls and scales in the dairy barn. Stalls at left and scales at right; drinking-water at right rear, permitting animal to drink while on scales. Floor elevated to provide for collection of excreta below.

FIG. 2 (B).—Rear of the metabolism stalls in the new quarters. View showing trap-doors for feces, one open, the other closed; also showing details of posts, planking, and construction of side-walls.

requirements of animals of different size, especially with regard to variation in length. The Pennsylvania Institute of Animal Nutrition measurably solved this problem after some years of investigation. Our own adaptation of their fundamental ideas arises from the experience of one of us (E. G. R.), who, on a several weeks' visit to the Institute of Animal Nutrition, was accorded every courtesy and the privilege of duplicating apparatus by Professor H. P. Armsby.

With regard to the width of our stalls, it was found that a relatively narrow stall (approximately 3 feet or 0.91 meter in width) would meet the requirements admirably for approximately full-grown animals while standing, but that considerably greater width was desirable for comfort to the animal while lying down, so that he could stretch his legs to prevent cramping. The Pennsylvania investigators built their stalls, therefore, on the principle that the lower half of the side-walls or partition of the stall, from the stanchion or rear end of the feed-box back, should be of sufficiently greater width than the upper part to meet these conditions. An adjustable feed-box and an adjustable screen shutter above the feed-box were used to vary the length of the stall.

On these essential principles the Durham stalls were designed, but with some modifications in the specifications of construction to meet the particular requirements and the rather limited space where our stalls had to be placed. While the rubber funnel was retained as the only possible means for collecting the urine from steers, the rubber duct for feces was dispensed with and a trap-door in the floor (see Fig. 2) was substituted. Flexible aprons were at first used to guard further against loss of feces, but these soon proved impracticable, as the animals found them irritating and broke them several times daily. It was also found that the animals soon learned that they could not back out of the stalls over an open trap, so that no additional provision was made in the rear of the stall to prevent them from backing out.

The only space available at the time when the stalls were first built was a corner in the basement in the section of the dairy barn[a] where the young dairy stock were kept. The space available was 24 feet long, 14 feet wide, and 9 feet high. As the floor of the basement, on which the stalls rested, was of concrete, there was no chance to place the collecting vessels underneath, thus complicating the problem somewhat because of the rather limited height available. (See Fig. 1.) It therefore became necessary to raise the stalls sufficiently above the concrete floor of the room so that containers of sufficient size could be placed under the stall floor and yet so that the animals would not at the same time be too near the ceiling when in the stalls. While more space, especially in height, would have been desirable, the plan as carried out under these conditions proved very satisfactory. Since this location was to be only temporary, it was decided to construct the stalls so that they could be easily taken apart without damage and moved, an advantage which actually was made use of after a year's work, when the stalls had to be moved to new quarters.

In the new quarters a sub-basement was available, but the stalls were put in place without any material alteration, except that the extra lengths of the 4

[a] For the privilege of using this space, as well as the space occupied by the respiration chamber, we are indebted to Professor J. M. Fuller.

by 4 inch uprights, which had been previously necessary to raise the stalls above the concrete floor, were cut off and closed boxes were hung under the floor to support the receptacles for feces (ordinary wash-boilers being used). These boxes were just large enough to accommodate the wash-boilers, giving as little unnecessary air-space as possible, and closely fitting hinged doors further reduced the chance for air currents and attendant evaporation. (See Fig. 5, p. 31.)

### GENERAL DESIGN AND MATERIALS USED IN METABOLISM STALLS.

The general design, therefore, combined three essential features which distinguished these stalls from ordinary stalls: (1) the sliding feed-box with adjustable shutters; (2) a padded floor with 1.5 inch opening near the center for urine hose; (3) side-walls or partitions, the lower half of which from the rear of the feed-box to the gutter gave at least 10 inches more width than the upper half; and (4) a specially designed trap for collection of feces. In the construction of the framework, 4 by 4 inch pieces were selected to serve as uprights or supporting posts for the floor and walls, six such pieces being used for each stall, namely, one in each corner, front and rear, and two in line with the side-walls at the rear end of the feed-box. The floor, consisting of 2 by 6 inch material, was then laid. The side-walls or partitions of the stall were put on in two independent sections, the lower half (also of 2 by 6 inch material) from the feed-box back being spiked on the *outside* of the supporting posts, while the upper half was nailed on the *inside* of the two respective stalls. A space of 2 inches was left between the corresponding inside posts of the two stalls, so that one single layer of 2 by 6 inch planking inserted in this space served as the lower half of the partition for both stalls. (See Fig. 2.) The upper half of the wall was constructed of $\frac{7}{8}$-inch matched sheathing, nailed on the inside of the supporting posts the entire length of the stalls, thus making the upper part narrower (due to the differential width of each wall section) by the thickness of the two 4-inch uprights plus the sheathing on both sides. (See Fig. 2.)

### FEED-BOXES AND ADJUSTABLE SHUTTERS.

The feed-boxes and adjustable shutters were designed to meet two requirements: (1) to prevent the scattering of feed so that all uneaten residue could be weighed back without loss, and (2) to lengthen or shorten the stall space by sliding the feed-box and the shutter above it backwards or forwards in order to accommodate animals of different lengths. Three sides of the feed-box were, therefore, built on a slant, so that the upper edges filled in the whole width of the stalls and fitted closely against the sides or stall partitions. Two cleats, nailed to the wall and resting over the top edge of the box, served as a guard-rail to steady it and at the same time prevented feed from being scattered through small cracks between the feed-box and the partition. (See Fig. 3.) As every possible precaution was necessary to prevent error in weighing the feed intake, the sides and front of the feed-box were constructed on an inward slant, thus reducing the floor area so that feed was not scattered over too much floor surface and sharp angles where feed could lodge out of reach of the animals were eliminated. Subsequent experience has shown the desirability of having these feed-boxes lined with galvanized sheet-iron.

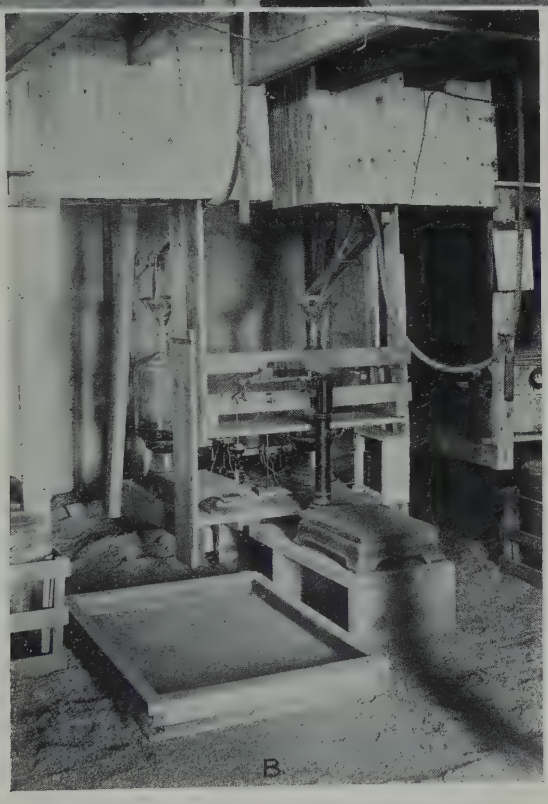


FIG. 3 (A).—Feed-boxes and adjustable shutters.
FIG. 4 (B).—View of basement beneath stalls.

The platforms supporting feces receptacles are shown; also boiler for feces collection, carboys and hose connections for urine collection, tray for mixing feces, and scales for weighing the aliquots.

The front of each stall was closed by a swinging shutter, fitted into the width of the stall and hung on the ceiling or on the cross-girders at the top of the stall just above the middle of the feed-box by means of strap hinges. Two 2 by 4 inch pieces were used as hangers to which boards were nailed to close the front. (See Fig. 3.) These shutters were made long enough to project about 2 or 3 inches into the feed-box, thus preventing waste out of the front of the box, as well as to allow varying the length of head-room by swinging backwards or forwards on hinges, the lower or free-swinging end being simply adjusted in different positions by means of ordinary door-bolts.

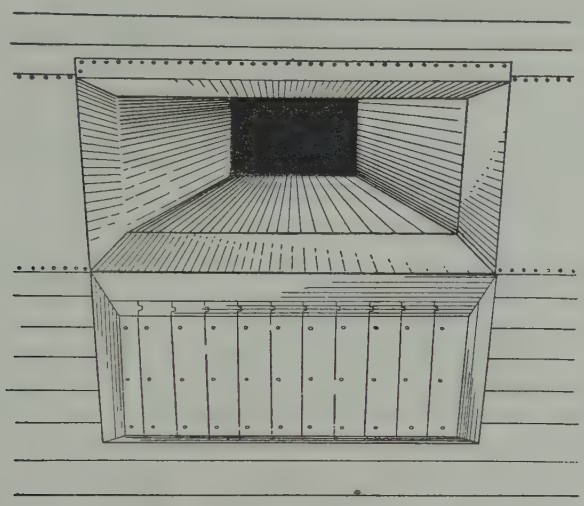

FIG. 5.—Trap for collecting feces.

TRAPS FOR COLLECTING FECES.

The general design of the trap for collecting feces is given in Fig. 5, which shows a view looking perpendicularly downwards from a position just in the rear of the animal. At the top edge or floor-level the width is 3 feet, i. e., 2 inches less than the inside width of the stall between the upright posts. The other surface dimension (longitudinal with stall) is 1 foot 5 inches. From the floor-level all four sides are built on a bevel down to a depth of 10 inches, to a rectangular opening 9 by 12 inches square, which has a straight drop 2 inches in depth. The trap-doors are fastened to the floor by means of strap hinges and the doors are kept open when the animal is in the stall and closed when he is to be taken out. The doors are fitted into the bevel so as to leave a surface flush with the rest of the floor when closed. These traps were simply built in between the cross-girders of the flooring, the bevel being made by filling in with fitted blocks of wood and the whole covered with medium weight galvanized-iron sheeting, the seams of which were carefully soldered so as to leave a smooth surface without leakage.

When the stalls were first placed in the dairy barn (see Fig. 1), the feces receptacles were supported about 3 inches above the concrete floor by small platforms provided with cleats along the side, so that the boilers could be slid into place without special effort in adjustment. These platforms were raised

sufficiently so that the boilers fitted fairly snugly against the trap above, but cleats were placed along the top sides of the boilers further to prevent air suction around the top of the receptacles, and to give even better air closure.

In the new quarters, where the stalls were finally located, a basement about 6½ feet in height was available and the receptacles for feces were therefore supported by platforms hung on the cross-girders underneath the stall floor, as shown in Fig. 4. These platforms were closed in with matched sheathing, so as to form close-fitting, air-tight boxes, supplied with hinged doors to prevent air-drafts between the basement and the stalls above.

Figure 4 also shows the receptacles (5-gallon carboys) used for urine collection and the half-inch hose conducting the urine from the funnel through the floor to the carboys. A loop in the hose is provided to give them a straight drop of approximately 3 feet directly below the floor opening, allowing sufficient slack for up-and-down movements without pinching, when the animals rise or lie down. It is of course important that this slack should always be taken up when an animal lies down, which is accomplished by hanging a 3-pound weight on the hose under the floor.

### APPLIANCES USED IN ALIQUOTING.

The gross daily weight of urine and feces was obtained on scales (metric) shown in Fig. 4. These scales had a capacity of 125 kg. and weighed accurately to 10 grams. This figure also shows the tray used in mixing feces, preparatory to aliquoting. It was 3 feet square and 2 inches deep, and covered inside and over the top with galvanized sheet-iron to prevent loss, which would have been materially greater if the surface had been of absorbent wood.

The aliquots, both of urine and feces, were weighed on a torsion balance, sensitive to 0.1 gram, glass beakers being used for weighing the urine samples and enameled flat dishes for the feces. Friction-top cans were used as containers for the aliquot samples of feces and glass-stoppered, 5-pint bottles for the aliquots of urine.

### SCALES FOR WEIGHING ANIMALS.

Since an essential of our work was to secure with the highest degree of accuracy the live weights of our animals, the scales[a] were selected with great care. They are provided with ball-bearing sockets upon which the platform rests and weigh accurately to half a pound. Indeed, when the animal maintains an absolutely quiet pose its weight can be read to a third or quarter of a pound. These scales were so located that the animals could be given drinking-water as they stood on the scale platform. Thus, the water intake could be obtained by weighing the animal before and after drinking. Running water is conducted through a pipe to the water-tub, so that the supply can be replenished while the animal is drinking. The tub is filled before the animal goes on the scales, but left covered until his live weight before drinking is obtained. The tub is then uncovered, so that the animal can drink, and while he is drinking the weight on the beam is slowly raised with the water intake, so that when he has finished the final weight can be obtained with great dispatch before the animal gets restless and tries to leave the scale platform.

[a] These scales are a standard product, designated as "coffee warehouse scales," having a capacity of 3,500 pounds and a platform 76 by 52 inches. They have given the greatest satisfaction.

## CHEMICAL METHODS OF ANALYSIS.

In connection with this research, analyses of feed, feces, urine, and expired air in the respiration chamber were necessary. Standard methods for the analysis of feed are in use in all of the agricultural experiment stations throughout the United States. These, as well as the standard methods for the analysis of feces, have been most carefully and critically studied, subjected to comparative tests, and finally specific directions for their procedures incorporated in "Official and tentative methods of analysis of the Association of Official Agricultural Chemists."[a] Certain specific modifications of or variations in method were occasionally necessary in the treatment of our special subjects, and these modifications are detailed in the following section.

### Sampling and Aliquoting.

Prior to the actual chemical analyses, special consideration must be given to the method of securing a representative sample; from urine this is extremely simple; from feed such as hay, for example, somewhat more complicated; and with feces, with their large mass and irregular moisture content, seemingly difficult. It is necessary to check daily measurements of excreta and feed with a composite sample representing aliquots for a definite length of time. Hence a method of aliquoting is essential. While on maintenance and during fattening the proportionate size of the aliquot samples of both feces and urine represented one-fiftieth of the total daily amount excreted; during the submaintenance periods,[b] when the total amounts voided were much less, larger samples were taken, representing in the case of both urine and feces one twenty-fifth of the total.

In aliquoting the feces and urine special precautions were necessary, and immediately after removal of urine and feces from the stall the containers were weighed with contents. The aliquot of urine, one twenty-fifth or one fiftieth, was then weighed, the bottles first being given a vigorous shaking. The aliquots were placed in a large, air-tight bottle with a few grams of chloroform to retard decomposition. The feces, when removed from the containers in which they were collected, were placed on a large flat tray, 3 feet square and 2 inches deep, where they were thoroughly mixed by the method recommended by Fries and Braman at the Pennsylvania State College, i. e., the whole mass was thoroughly mixed as a mason mixes mortar, then flattened out into a square layer about 2 or 3 inches thick, and divided into quarters, the four quarters being piled on top of each other and the whole mass again mixed. This operation was repeated three times and the aliquot part was taken with a small trowel in approximately equal amounts from each of the four quarters, after the feces had been quartered the fourth time. Undeniably during this procedure a certain amount of moisture was unavoidably lost by evaporation. No correction has been made for this.

The daily aliquots were placed in large, air-tight tin cans provided with friction tops to prevent further loss of moisture. A few grams of carbon bisulphide were then added as a preservative. After 14 consecutive aliquots had been secured, representing a 2-week period, this composite of feces,

[a] The edition which is revised to November 1, 1919, and published in September, 1920, includes practically all of these methods.

[b] Period 2 of submaintenance was an exception, as only one-fiftieth of the total was used.

along with the corresponding composite of urine, was taken to the chemical laboratory where they were weighed prior to analysis. The urine bottles were then thoroughly shaken and samples were taken for the determination of nitrogen and dry matter. The feces were removed from their containers and placed in a mixing tray, where the aliquots were thoroughly mixed, as was done with each day's total feces, and a sample was taken for the determination of moisture and nitrogen, a large sample at the same time being brought to air-dry condition for preservation.

### Analysis of Fresh Urine.

*Moisture.*—From the aliquot samples of urine as they were delivered to the laboratory 10 c. c. samples were pipetted into previously dried and weighed bottles, which were then immediately weighed and placed in a vacuum desiccator over sulphuric acid. The desiccators were exhausted every second day and the samples dried until they were constant in weight. In order to correct for the loss in dry matter due to the decomposition of urea, total nitrogen determinations were made upon the dried residue from the moisture determination. The loss in nitrogen due to drying was converted by a factor into urea and the urea thus lost was added to the dry-weight determinations.

*Determination of nitrogen.*—Using the same pipette which was used in the moisture determinations, 10 c. c. samples of urine were transferred to Kjeldahl flasks, the weight of these samples being readily derived from the weight of equivalent samples for moisture determinations. The determination of nitrogen was then carried out according to the Kjeldahl-Gunning method, as follows: 5 grams potassium sulphate, 25 c. c. concentrated sulphuric acid C. P., 10 c. c. mercuric sulphate-copper sulphate solution[a] (containing 1 gram mercuric sulphate and 1 gram copper sulphate per 10 c. c.) were added to the Kjeldahl flask. The contents were then digested until water had been removed, and then 15 grams more potassium sulphate added and the samples digested until this solution was clear and then boiled for 1½ hours longer. After digestion was completed and the flasks had partially cooled, 250 c. c. distilled water were added to each flask. Granulated zinc, paraffine, potassium-sulphide solution, and sodium-hydroxide solution were added according to the usual procedure, and the ammonia distilled into standard sulphuric acid, the final titration being made with decinormal sodium-hydroxide solution, using cochineal as an indicator.

*Nitrogen in dried residue from moisture determinations.*—These residues were carefully transferred to cool flasks and the nitrogen determined by precisely the method outlined above.

### Analysis of Fresh Feces.

*Moisture.*—In the nitrogen balances contemplated, it was felt that in view of the well-known loss of ammonia in drying feces as well as urine, all nitrogen determinations must be made upon fresh substances, and consequently not only nitrogen but moisture was thus determined. In the moisture determinations, representative samples of 8 to 12 grams of fresh feces were transferred to weighing-bottles which had previously been dried and weighed. The bot-

[a] In making the mercuric sulphate-copper sulphate solution, sulphuric acid was added to bring the mercuric sulphate into solution.

tles were immediately weighed after the addition of samples and transferred to vacuum desiccators over sulphuric acid. The desiccators were exhausted each day and the samples were dried until constant in weight.

*Nitrogen determination in fresh feces.*—A representative sample of the fresh feces was placed in a weighing-bottle and weighed. After removing the samples, which were transferred to the Kjeldahl flask, the bottles were again weighed and the weight of the samples determined by difference. The total nitrogen in the feces was then determined by the same method as that employed in determining nitrogen in fresh urine.

### Methods of Analysis of Air-dried Feeds and Feces.

*General analysis.*—Moisture, ether extract, crude fiber, and ash were all determined by the methods given in the "Official and tentative methods of analysis of the Association of Official Agricultural Chemists" (1920).[a] Protein was determined in the same way as the nitrogen in fresh feces.

*Method of preparation of air-dry samples.*—The hay samples were run through a chopper, which cut the hay into pieces of about 2 inches in length. A weighed sample of about 500 grams of this material was transferred to an oven at 60° C. After several days the sample was removed to room conditions and allowed to become air-dried. The samples were then weighed and the loss in moisture, which was necessary to bring the sample to air-dried condition, was determined. The sample was then ground fine in the feed-mill and the moisture was determined in a 2-gram sample of this material by heating it at 100° C. in a water-jacketed oven until constant in weight. The feces samples were similarly dried in an oven at 60° C. and subjected exactly to the treatment outlined above prior to final analysis of air-dry matter.

The chemical analyses of all of these feeding-stuffs, as well as the complete analyses of feces and the determination of nitrogen in urine, were made under the direction of Dr. H. R. Kraybill, chemist of the New Hampshire Agricultural Experiment Station, for whose interest and cooperation in the work we are very grateful.

At the Nutrition Laboratory a calorimetric bomb[b] was available, so that direct heats of combustion could be made on many of the samples, including two samples of hay and cottonseed meal, and particularly a number of samples of feces. For these determinations we are indebted to Mrs. Cornelia Golay Benedict, who made them with the assistance of Miss Mary D. Finn and Miss Marion L. Baker.

## NATURE, COMPOSITION, AND AMOUNTS OF FEEDING-STUFFS.

During the two years' work the main feeding-stuff used was hay, but in the refeeding or fattening periods grain mixtures of various proportions were used. Since particular stress in the investigation was laid upon the physiological effects of maintenance at a low nutritive level, not quite so much attention was paid to the complete analysis of the feed samples as was perhaps desirable, and no analyses of feces or urine were made during the first year's work. For the final computation of the results upon all the animals we have incorporated in

[a] Moisture and ash, p. 71; ether extract, p. 72; crude fiber, pp. 97, 98.
[b] Benedict and Higgins, Journ. Am. Chem. Soc., 1910, 32, p. 461.

Table 2 the chemical composition of the water-free substance in the various feeds used. Much of this admittedly has had to be in the nature of assumed figures from average results, and hence in Table 2 the figures which represent actual determinations made in connection with this research are italicized.

TABLE 2.—*Chemical composition of water-free substance in feeds.*

| Feed. | Steers. | Periods. | Ash. | Ether extract. | Crude fiber. | Nitrogen. | Protein. | Nitrogen-free extract. | Energy per gram. |
|---|---|---|---|---|---|---|---|---|---|
| | | | *p. ct.* | *p. ct.* | *p.ct.* | *p. ct.* | *p. ct.* | *p. ct.* | *cal.* |
| Hay I | 1 to 12 | All | *4.51* | *2.28* | *34.39* | *1.13* | 7.07 | 51.75 | 4.455 |
| Hay II | A and B | 1 to 12 | *5.85* | *2.76* | *28.34* | *1.09* | 6.83 | 56.22 | *4.466* |
| Hay III | Do | 13 to 16 | 5.85 | 2.76 | 28.34 | *1.17* | 7.32 | 55.73 | *4.444* |
| Wheat bran | Do | Do | 6.97 | 5.18 | 9.99 | *2.65* | 15.13 | 62.73 | 4.532 |
| Cornmeal | Do | Do | 1.65 | 5.14 | 2.34 | *1.59* | 9.53 | 81.34 | 4.505 |
| Linseed meal | Do | Do | 6.71 | 7.07 | 8.86 | *5.02* | 27.62 | 49.74 | 5.102 |
| Cottonseed meal | Do | Do | 5.91 | 7.87 | 12.09 | *7.49* | 41.21 | 32.92 | *4.971* |

Three samples of hay were used: Hay I, that for steers 1 to 12 during 1918–19; Hay II, that for steers A and B for periods 1 to 12; and Hay III, of a very similar composition, that used for the same animals for periods 13 to 16. Bran, cornmeal, linseed meal, and cottonseed meal were used in various mixtures, the proportions of which will be discussed later on. Of these concentrates, direct determinations were made only of the nitrogen, and, in one instance (cottonseed meal), of the heat of combustion.

Complete analyses of hay and feces were made, chiefly to determine the fundamental point as to the digestibility of the various ingredients of hay when the steers were on full and submaintenance hay rations. The hay used was a native product. In order to obtain as nearly uniform conditions as possible, the hay used throughout the experiments was obtained from the same farm, which produced a typical class of hay of very uniform character, generally known as "native hay" in practical parlance. In fact, this farm had served the purpose of producing hay for a number of years, so that the grasses from which the hay was made would naturally have been of a very uniform character, as was evident on inspection. No microscopic analysis of this hay was made, but as a result of several independent estimates, including especially that of the owner of the farm on which the hay was grown, it appeared that the hay was approximately 75 per cent timothy (*Phleum pratense*), the remainder being composed in about equal proportions of various mixed grasses of the finer type, including witch grass (*Panicum capillare*), June grass (*Poa pratensis*), and redtop (*Agrostis alba*). Due to the fact that the land had been somewhat run down, the timothy hay did not head out. The hay for steers A and B was the same kind and practically the same thing as that for steers 1 to 12, except that it was cut a year later.

Reference to Table 2 shows that the analyses of the hays for steers 1 to 12 and steers A and B differ essentially only in their crude-fiber content. The nitrogen content is essentially constant and there is but a slight difference in the fat content, with, however, a little over 1 per cent greater ash content in the hay for steers A and B. Unfortunately, the heat of combustion of Hay I

was not directly determined, and hence we are assuming for the energy per gram of water-free substance in the hay for steers 1 to 12 the average of two determinations for steers A and B, namely, 4.455 calories per gram. For Hay III it was assumed that the percentages of ash, ether extract, and crude fiber were the same as in Hay II, and hence only the nitrogen content and heat of combustion were directly determined. As stated above, the determinations of ash, ether extract, crude fiber, and nitrogen were made primarily to secure evidence with regard to the digestibility of hay.

With regard to the wheat bran, only nitrogen was directly determined. The other percentages have been computed from data given in different experiment-station bulletins.[a] The figure for the heat of combustion represents the average of some results reported by Armsby.[b] Cornmeal was whole dent corn, ground, and here again only nitrogen was directly determined, the other compositions being assumed.[c] The figure for the heat of combustion was taken from data given by Professor Armsby.[d] Linseed meal was old-process meal, and again only the nitrogen was determined, the remaining compositions being assumed[e] and the value for the heat of combustion being taken from data given by Armsby.[f]

With the cottonseed meal the nitrogen content and the heat of combustion were determined, the remaining compositions being assumed from data in different experiment-station bulletins.[a] Our experience in securing the probable heat of combustion of cottonseed meal per gram is worthy of record. It appears that there are extraordinarily few determinations of the heat of combustion of cottonseed meal in print, and we devoted a great deal of time to locating these before the actual determinations of our sample were made by Mrs. Benedict. The only values that we have found recorded are those by Armsby,[g] who gives an average value of 4.930 calories per gram of water-free substance, a value which corresponds very closely to that found by Mrs. Benedict (4.971). Obviously, with a substance as rich in fat as cottonseed meal, slight differences in the heat of combustion are to be expected. It was only when we noted the extreme paucity of data with regard to the heat of combustion that we decided to have this determined. For our own results the value found by Mrs. Benedict was used in all cases.

In computing the protein from the nitrogen, a process necessary in the indirect computation of the nitrogen-free extract, we multiplied the total nitrogen, as determined by the Kjeldahl method, by the following factors: for hay, 6.25; wheat bran, 5.7; cornmeal, 6; linseed meal, 5.5; and cottonseed meal, 5.5.[h]

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[a] Kraybill and Smith, New Hampshire Station Bull. 195, 1920, pp. 21, 22, and 34 to 41; also, Smith and Bradley, Massachusetts Station Bull. 13, 1920, pp. 7 and 8.

[b] Armsby and Fries, U. S. Dept. Agric., Bureau Animal Industry Bull. 128, 1911, p. 31; *ibid.*, Journ. Agric. Research, 1915, 3, p. 438.

[c] Smith and Bradley, Massachusetts Station Bull. 13, 1920, p. 8; also, Henry and Morrison, Feeds and feeding, Madison, Wisconsin, 1916, 16th ed., p. 633.

[d] Armsby, Fries, and Braman, Journ. Agric. Research, 1916, 7, p. 380.

[e] Kraybill and Smith, New Hampshire Station Bull. 195, 1920, p. 27.

[f] Armsby and Fries, U. S. Dept. Agric., Bureau Animal Industry Bull. 51, 1903, p. 11; also, Armsby, U. S. Dept. Agric., Bureau Animal Industry Bull. 459, 1916, p. 8.

[g] Armsby and Fries, Journ. Agric. Research, 1917, 11, p. 465.

[h] Armsby and Fries, U. S. Dept. Agric., Bureau Animal Industry Bull. 128, 1911, p. 203; also Armsby and Fries, Journ. Agric. Research, 1917, 11, p. 465.

TABLE 3.—*Total water-free substance in feed[1] eaten, Groups I, II, and III. (Average values per day.)*

| Date. | Group I. | | | Group II. | | | | | Group III.[2] | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | No. 2 | No. 4 | No. 5 | No. 1 | No. 3 | No. 7 | No. 10[3] | No. 11 | No. 6[4] | No. 8 | No. 9[4] | No. 12 |
| 1918–1919 | *kg.* | *kg.* | *kg.* | *kg.* | *kg.* | *kg.* | *kg.* | *kg.* | *kg.* | *kg.* | *kg.* | *kg.* |
| Nov. 27 to Dec. 1 | 9.2 | 10.4 | 11.3 | 11.0 | 10.6 | 8.0 | 11.8 | 8.2 | 7.6 | 9.9 | 10.9 | 8.3 |
| Dec. 2 Dec. 8 | 6.4 | 8.2 | 8.4 | 8.2 | 8.3 | 6.2 | 8.7 | 7.3 | 5.9 | 7.7 | 8.6 | 6.6 |
| Dec. 9 Dec. 15 | 7.3 | 8.3 | 9.2 | 9.0 | 8.4 | 6.9 | 9.3 | 8.2 | 6.9 | 8.2 | 9.0 | 6.9 |
| Dec. 16 Dec. 21 | 7.6 | 8.2 | 9.1 | 8.8 | 8.3 | 7.1 | 9.1 | 8.0 | 7.2 | 8.2 | 8.7 | 7.1 |
| Dec. 22 Dec. 27 | 7.6 | 8.2 | 9.0 | 4.9 | 4.5 | 3.9 | 4.9 | 4.4 | 5.3 | 5.7 | 6.2 | 5.2 |
| Dec. 28 Jan. 5 | 6.5 | 7.2 | 8.1 | 4.1 | 3.7 | 3.2 | 4.1 | 3.2 | 4.8 | 4.9 | 5.6 | 4.0 |
| Jan. 6 Jan. 12 | 6.5 | 7.2 | 8.1 | 4.1 | 3.7 | 3.2 | 4.1 | 3.3 | 4.7 | 4.9 | 5.6 | 4.1 |
| Jan. 13 Jan. 19 | 6.5 | 7.3 | 8.1 | 3.9 | 3.7 | 3.1 | 4.1 | 3.2 | 4.8 | 4.9 | 5.6 | 3.9 |
| Jan. 20 Jan. 26 | 6.5 | 7.2 | 8.1 | 4.1 | 3.7 | 3.2 | 4.1 | 3.2 | 4.8 | 4.9 | 5.7 | 4.0 |
| Jan. 27 Feb. 2 | 6.4 | 7.2 | 8.2 | 4.1 | 3.7 | 3.3 | 4.1 | 3.3 | 4.8 | 4.9 | 5.7 | 4.1 |
| Feb. 3 Feb. 9 | 6.4 | 7.2 | 8.1 | 4.1 | 3.7 | 3.2 | 4.1 | 3.3 | 4.8 | 4.9 | 5.7 | 4.1 |
| Feb. 10 Feb. 16 | 6.5 | 7.2 | 8.1 | 4.1 | 3.7 | 3.3 | 4.1 | 3.3 | 2.8 | 2.9 | 3.8 | 2.4 |
| Feb. 17 Feb. 23 | 6.5 | 7.3 | 8.1 | 4.1 | 3.7 | 3.3 | 4.1 | 3.3 | 2.9 | 2.9 | 3.8 | 2.5 |
| Feb. 24 Mar. 2 | 6.6 | 7.3 | 8.1 | 4.1 | 3.7 | 3.3 | 4.1 | 3.3 | 2.8 | 2.9 | 3.8 | 2.5 |
| Mar. 3 Mar. 9 | 6.5 | 7.3 | 8.2 | 4.1 | 3.7 | 3.3 | 4.1 | 3.3 | 2.9 | 2.9 | 3.8 | 2.4 |
| Mar. 10 Mar. 16 | 6.7 | 7.4 | 8.4 | 4.1 | 3.7 | 3.3 | 4.1 | 3.3 | 2.8 | 2.9 | 3.8 | 2.5 |
| Mar. 17 Mar. 23 | 6.9 | 7.7 | 8.5 | 4.1 | 3.7 | 3.3 | 4.1 | 3.3 | 2.8 | 2.9 | 3.8 | 2.5 |
| Mar. 24 Mar. 30 | 6.9 | 7.6 | 8.5 | 4.1 | 3.7 | 3.3 | 4.1 | 3.3 | 2.8 | 2.9 | 3.8 | 2.5 |
| Mar. 31 Apr. 6 | 6.9 | 7.6 | 8.6 | 4.0 | 3.7 | 3.3 | 4.1 | 3.3 | 2.9 | 2.9 | 3.8 | 2.5 |
| Apr. 7 Apr. 13 | 6.9 | 7.4 | 8.5 | 4.0 | 3.7 | 3.3 | 4.1 | 3.3 | 2.8 | 2.9 | 3.8 | 2.5 |
| Apr. 14 Apr. 20 | 6.8 | 7.7 | 8.5 | 4.1 | 3.7 | 3.3 | 4.1 | 3.2 | 2.8 | 2.9 | 3.7 | 2.4 |
| Apr. 21 Apr. 27 | 6.9 | 7.6 | 8.6 | 3.9 | 3.7 | 3.3 | 4.1 | 3.3 | 2.9 | 2.9 | 3.8 | 2.4 |
| Apr. 28 May 5 | 6.7 | 7.5 | 8.4 | 3.5 | 3.7 | 3.3 | 4.1 | 3.3 | 2.8 | 2.9 | 3.8 | 2.4 |
| May 6 May 12 | 7.9 | 7.1 | 10.5 | 8.0 | 8.8 | 6.1 | 5.6 | 6.5 | 6.4 | 6.5 | 8.1 | 6.3 |
| May 13 May 19 | 5.9 | 9.6 | 10.2 | 10.2 | 8.9 | 7.6 | 6.8 | 8.9 | [5]3.1 | 8.2 | [5]3.8 | 7.4 |
| May 20 May 26 | ..... | 9.6 | 11.1 | 10.4 | 7.9 | 9.0 | 7.6 | 9.8 | ..... | 9.8 | ..... | 8.0 |
| May 27 June 2 | ..... | 10.1 | 11.2 | 8.8 | 10.3 | 7.7 | 7.6 | 8.5 | ..... | 9.0 | ..... | 8.1 |
| June 3 June 9 | ..... | 10.6 | 11.4 | 9.7 | 9.7 | 8.8 | 7.5 | 10.4 | ..... | 10.2 | ..... | 8.9 |
| June 10 June 16 | ..... | 11.3 | 12.3 | 9.9 | 12.3 | 7.8 | 7.5 | 10.0 | ..... | 12.6 | ..... | 10.2 |
| June 17 June 23 | ..... | 12.8 | 13.7 | 9.5 | 11.9 | 7.4 | 6.9 | 9.8 | ..... | 10.9 | ..... | 8.7 |
| June 24 June 30 | ..... | 11.8 | 14.4 | 11.4 | 14.0 | 10.0 | 7.6 | 12.5 | ..... | 12.4 | ..... | 10.2 |
| July 1 July 7 | ..... | 12.1 | 14.0 | 14.0 | 14.8 | 9.8 | 8.2 | 12.4 | ..... | 13.5 | ..... | 9.7 |
| July 8 July 14 | ..... | 13.6 | 14.9 | 12.9 | 13.7 | 12.0 | 13.9 | 9.3 | ..... | 12.1 | ..... | 10.1 |
| July 15 July 21 | ..... | 14.9 | 15.4 | 15.0 | 16.2 | 13.0 | 12.5 | 13.2 | ..... | 14.6 | ..... | 10.7 |
| July 22 July 28 | ..... | 15.1 | 15.4 | 15.6 | 16.1 | 13.5 | 11.9 | 13.5 | ..... | 14.5 | ..... | 11.0 |
| July 29 Aug. 4 | ..... | 15.3 | 15.8 | 15.0 | 16.2 | 14.3 | 14.6 | 15.1 | ..... | 14.5 | ..... | 11.9 |
| Aug. 5 Aug. 11 | ..... | 14.7 | 15.2 | 14.9 | 15.6 | 13.1 | 16.0 | 14.0 | ..... | 14.0 | ..... | 11.6 |
| Aug. 12 Aug. 18 | ..... | 16.3 | 16.4 | 15.3 | 16.1 | 13.5 | 16.5 | 14.4 | ..... | 15.5 | ..... | 12.9 |
| Aug. 19 Aug. 25 | ..... | 16.3 | 16.0 | 15.8 | 16.2 | 13.7 | 16.9 | 14.2 | ..... | 15.4 | ..... | 12.9 |
| Aug. 26 Sept. 1 | ..... | [6]12.2 | [6]12.3 | 15.5 | 15.9 | 13.5 | 15.9 | 11.2 | ..... | 14.9 | ..... | 12.9 |
| Sept. 2 Sept. 8 | ..... | ..... | ..... | 11.2 | 13.7 | 11.6 | 15.3 | 13.3 | ..... | 13.0 | ..... | 12.6 |
| Sept. 9 Sept. 15 | ..... | ..... | ..... | 13.2 | 15.1 | 11.3 | 15.1 | 13.0 | ..... | 13.5 | ..... | 9.8 |
| Sept. 16 Sept. 22 | ..... | ..... | ..... | 13.4 | 16.1 | 13.1 | 17.0 | 13.5 | ..... | 13.7 | ..... | 12.7 |
| Sept. 23 Sept. 29 | ..... | ..... | ..... | 14.6 | 16.2 | 11.1 | 17.2 | 12.8 | ..... | 13.3 | ..... | 9.6 |
| Sept. 30 Oct. 6 | ..... | ..... | ..... | 15.1 | 15.9 | 12.8 | 18.4 | 12.9 | [7]2.1 | 14.0 | [7]1.9 | 12.3 |
| Oct. 7 Oct. 13 | ..... | ..... | ..... | 15.1 | 15.9 | 13.0 | 18.2 | 13.6 | [7]2.8 | 13.7 | [7]3.1 | 12.5 |
| Oct. 14 Oct. 20 | ..... | ..... | ..... | 13.7 | 13.7 | 11.2 | 15.6 | 10.8 | [7]2.9 | 8.7 | [7]3.9 | 9.9 |
| Oct. 21 Oct. 27 | ..... | ..... | ..... | 14.2 | 15.2 | 10.1 | 16.0 | 10.8 | [7]2.8 | 10.9 | [7]3.5 | 10.7 |
| Oct. 28 Nov. 3 | ..... | ..... | ..... | 6.8 | 11.5 | 9.9 | 17.8 | 12.1 | [8]9.7 | 12.5 | [8]11.4 | 11.6 |

[1] Feed was hay alone until May 13, when most of the steers were given both hay and grain.

[2] With Group III certain of the values do not represent exactly the dates given in the first column. Thus, in December, February, and October, the data were averaged for the following periods: Dec. 22–29, Dec. 30–Jan. 5, Feb. 3–7, Feb. 8–16, Oct. 21–28, and Oct. 29–Nov. 3.

[3] Steer 10 received hay alone until July 8, when he began to receive both hay and grain.

[4] Steers 6 and 9 were on pasture from May 13 to Oct. 28 inclusive, after which date, due to the onset of cold weather, they were stall-fed on both hay and grain.

[5] Water-free substance in hay per day, May 13 to 16 inclusive; steer also on pasture.

[6] For Aug. 26 and 27 only.

[7] Water-free substance in hay per day, Oct. 5 to 28 inclusive; steer also on pasture.

[8] Represents total water-free substance in both hay and grain, Oct. 29 to Nov. 3 inclusive. Steers were brought back from pasture on Oct. 28.

For our special purpose in this report—that is, considering that a very large proportion of our experiments were made on hay alone, it is obvious that the hay analyses have the greater significance. They will be used extensively in subsequent computations of the digestibility and metabolizable energy.

The amounts of water-free substance in feed consumed on the average per day by steers 1 to 12 throughout the entire period of observation are recorded in Table 3 and similar data are given for steers A and B in Table 4. In Table 4 the amounts of the individual feedstuffs are shown, but in Table 3 it has not been deemed necessary to report the amounts of hay and grain separately, particularly since the feed consisted entirely of hay alone for all the animals until May 13.

TABLE 4.—*Water-free substance in feed eaten, steers A and B. (Average values per day.)*

| Period. | Date.[1] | Steer A. | | | | Steer B. | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | Hay. | Bran. | Corn-meal. | Total. | Hay. | Bran. | Cotton-seed meal. | Linseed meal. | Total. |
| | 1919-20 | *kg.* | *kg.* | *kg.* | *kg.* | *kg.* | *kg.* | *kg.* | *kg.* | *kg.* |
| 1 | Dec. 27 to Jan. 10 | 6.84 | ..... | ..... | 6.84 | 6.50 | ..... | ..... | ..... | 6.50 |
| 2 | Jan. 10 Jan. 24 | 4.09 | ..... | ..... | 4.09 | 4.09 | ..... | ..... | ..... | 4.09 |
| 3 | Jan. 24 Feb. 7 | 4.10 | ..... | ..... | 4.10 | 4.05 | ..... | ..... | ..... | 4.05 |
| 4 | Feb. 7 Feb. 21 | 4.10 | ..... | ..... | 4.10 | 4.10 | ..... | ..... | ..... | 4.10 |
| 5 | Feb. 21 Mar. 6 | 3.81 | ..... | ..... | 3.81 | 3.81 | ..... | ..... | ..... | 3.81 |
| 6 | Mar. 6 Mar. 20 | 3.87 | ..... | ..... | 3.87 | 3.87 | ..... | ..... | ..... | 3.87 |
| 7 | Mar. 20 Apr. 3 | 3.61 | ..... | ..... | 3.61 | 3.61 | ..... | ..... | ..... | 3.61 |
| 8 | Apr. 3 Apr. 17 | 3.48 | ..... | ..... | 3.48 | 3.61 | ..... | ..... | ..... | 3.61 |
| 9 | Apr. 17 May 1 | 3.61 | ..... | ..... | 3.61 | 3.61 | ..... | ..... | ..... | 3.61 |
| 10 | May 1 May 15 | 3.61 | ..... | ..... | 3.61 | 3.61 | ..... | ..... | ..... | 3.61 |
| 11 | May 15 May 29 | 3.61 | ..... | ..... | 3.61 | 3.61 | ..... | ..... | ..... | 3.61 |
| 12 | May 29 June 12[2] | 7.91 | ..... | ..... | 7.91 | 7.91 | ..... | ..... | ..... | 7.91 |
| 13 | Oct. 22 Nov. 5 | 8.10 | 0.98 | 1.92 | 11.00 | 8.04 | 0.98 | 0.99 | 0.98 | 10.99 |
| 14 | Nov. 5 Nov. 19 | 8.48 | 1.80 | 3.50 | 13.78 | 8.39 | 1.80 | 1.81 | 1.80 | 13.80 |
| 15 | Nov. 19 Dec. 3 | 5.16 | 2.49 | 4.83 | 12.48 | 5.50 | 2.70 | 2.72 | 2.70 | 13.62 |
| 16 | Dec. 3 Dec. 17 | 5.59 | 2.51 | 4.88 | 12.98 | 5.17 | 2.70 | 2.72 | 2.70 | 13.29 |

[1] The periods begin and end at 2 p. m. on the respective dates.

[2] The steers were on pasture from June 13 to Oct. 15 inclusive, and were fed in their stalls on hay alone (amount not recorded) from Oct. 16 to 21 inclusive.

*Salt.*—Ordinary stock salt was used. A rough computation indicates that each animal received approximately 50 grams per day. This was not, however, accurately weighed, and the quantitative estimates apply only to steers A and B, for the amount given to these two animals from December 27 to June 12 was 18 kg. Every second or third day they were given a small handful. From the total amount purchased and used and the number of days the estimate of 50 grams per day per head was made.

## EARLIER RESPIRATION STUDIES WITH LARGE ANIMALS.

In the determination of the gaseous metabolism of both men and animals various types of respiration apparatus of different sizes have been employed. Most of these were of a size suitable only for small laboratory animals, but in some instances they were large enough for sheep and, indeed, for men. For the purpose of this particular discussion we will disregard all of the apparatus for smaller animals as well as apparatus designed primarily for men,

and will consider only those constructed for gaseous metabolism studies with large domestic animals, primarily horses and steers.

*Lassaigne, 1846–1849.*[a]—The earliest record of respiration experiments with large animals is the work of Lassaigne, of Paris. He studied the carbon-dioxide production of several horses and a steer, besides other smaller animals, by leaving the animal in a small, hermetically closed stall of known content for a certain length of time and analyzing the air for carbon dioxide at the beginning and end of each experiment. In one experiment two horses of average size were inclosed in a stall having a volume of 78.5 cubic meters for 45 minutes. At the end of this time samples of air were taken in two bottles, one on the floor of the stall and one near the ceiling, and later analyzed over mercury, the carbon dioxide being absorbed by soda-lime and the oxygen by phosphorus. In computing the total amount of carbon dioxide produced by the animal in the stall, correction was made for the amount usually found in the atmosphere. Other determinations of carbon-dioxide production were made in a stall of 47,340 liters capacity, the horse remaining in the stall for a period of 1 hour and measurements being made before and after exercise.

*Grouven, 1864.*[b]—Eighteen years after Lassaigne's publication, Grouven, in Salzmünde, described a respiration chamber which he constructed for steers. His apparatus was somewhat similar to the Pettenkofer apparatus for men in Munich, but differed in many respects, since, as he states, it was under process of construction 1½ years before he was aware of the existence of the Pettenkofer apparatus. His chamber was made of sheets of tin-plate, with an outer casing of wood. It had a capacity of 9.4 cubic meters, and the ventilation rate was 30 cubic meters per hour. The chamber was connected with two different equipments, one for determining ammonia, hydrogen sulphide, and the "vom Thiere perspirirten condensirbaren organischen Gase" in the products of respiration—the other for determining the carbon-dioxide production. The carbon dioxide produced by the animal was determined by passing through baryta water a small aliquot of the air leaving the chamber. Urine was collected outside the chamber by means of a urine funnel, and the feces were collected in a large rubber sack attached to the animal.

It is of interest here to cite the four respiration experiments carried out by Grouven with his apparatus, experiments which, as he states, are the first up to 1863 to have been made with animals of the size of a steer. All four experiments were made with a steer weighing 550 kg. and feed was given to the steer during the course of the experiment. The results are summarized in Table 5, herewith.

It is somewhat surprising to find that Grouven's work has been so long neglected by writers on animal nutrition. Indeed, in English we know of but one place where it is adequately cited—that is, in the admirable "Digest of metabolism experiments" by Professor W. O. Atwater and Dr. C. F. Langworthy.[c] As part explanation of this seeming neglect of Grouven's rather remarkable work should be cited the severe critique of Henneberg,[d] whose

[a] Lassaigne, Journ. de Chimie médicale, 1846, 2, pp. 477 and 751; *ibid.*, 1849, 5, pp. 13 and 253. Also, Journ. f. praktische Chemie, 1849, 46, p. 287; *ibid.*, 1849, 47, p. 136.

[b] Grouven, Physiologisch-chemische Fütterungsversuche. Zweiter Bericht über die Arbeiten der agrikulturchemischen Versuchsstation zu Salzmünde, Berlin, 1864, pp. 207 et seq.

[c] Atwater and Langworthy, U. S. Dept. Agric., Office Expt. Sta. Bull. 45, 1898, pp. 288–293, 299.

[d] Henneberg, Journ. f. Landw., 1865, 13, p. 89.

views undoubtedly dominated the thoughts of most Continental writers to the complete exclusion of serious consideration of Grouven's ideas. It is, however, worthy of note that, although many of Grouven's conclusions were based upon theoretical conceptions rather than upon attested facts, he still presents in his volume many ideas which are to-day accepted as the best expressions of the true processes of animal nutrition.

TABLE 5.—*Carbon-dioxide production of a 550-kg. steer (Grouven).*[1]

| Date. | Length of experiment. | Average temperature of chamber. | Carbon dioxide produced. | | Ration. |
|---|---|---|---|---|---|
| | | | During experiment. | Per 24 hours. | |
| 1863 | *hrs.* | *°C.* | *gm.* | *gm.* | |
| Dec. 8 | 12 | 21.5 | 2,295 | 4,590 | 4,000 gm. straw; 50 gm. salt. |
| Dec. 9 | 12 | 21.6 | 2,235 | 4,470 | Do. |
| Dec. 11 | 8 | 21.0 | 1,504 | 4,510 | 4,000 gm. straw; 50 gm. salt; 2,500 gm. cane sugar. |
| Dec. 12 | 8 | 20.7 | 1,612 | 4,835 | Do. |

[1] Grouven, loc. cit., pp. 267 and 268.

Among other points, it is to be noted that Grouven actually fasted a full-grown steer for 8 days and 5 other steers for shorter periods of from 2 to 5 days, although no gaseous-metabolism measurements were made under these conditions. Still, most important observations with regard to loss in body-weight, pulse-rate, respiration-rate, amount of urine and feces excreted and water consumed, temperature of the stall, and likewise analyses of feces and urine under conditions of fasting, were recorded by him—observations that, so far as we are at present aware, have been wholly ignored in all subsequent considerations of this important factor of fasting with large animals. Inasmuch as we are at the moment of writing engaged at the Agricultural College Experiment Station at Durham, New Hampshire, in an extensive study of the influence of fasting upon full-grown steers, further consideration of Grouven's results will be deferred until our data are ready for publication.

*Henneberg, 1869.*[a]—At the Agricultural Experiment Station at Weende-Göttingen, Henneberg and his associates constructed the first respiration chamber for large animals modeled in all essential details after the original Pettenkofer respiration apparatus in Munich. The Weende chamber, made of sheet-iron, was larger than its prototype, having a capacity of 17.5 cubic meters as against 12 cubic meters. With it numerous investigations were carried out with steers and sheep, in which direct determinations were made of the carbon-dioxide production, moisture in expired air, methane, and hydrogen.

This same chamber was later made use of by Lehmann, Hagemann, and Zuntz,[b] who in the fall of 1891 carried out some respiration experiments with

[a] Henneberg, Kühn, Märcker, Schulze, and Schultze, Journ. f. Landw., 1869, 16, p. 176. Same article also published in Henneberg's Neue Beiträge zur Begründung einer rationellen Fütterung der Wiederkäuer, Göttingen, 1870, pt. 1, pp. 5 et seq.

[b] Lehmann, Hagemann, and Zuntz, Landw. Jahrb., 1894, 23, p. 125.

their "Berlin horse" at the Göttingen station. In the Berlin experiments they had employed a tracheal canula in determining the carbon-dioxide production and oxygen consumption. In Göttingen they combined with the respiration chamber their tracheal canula equipment, so that they could determine the respiratory exchange simultaneously by the chamber and the canula method. The apparatus for measuring the carbon-dioxide production, the pump valves, baryta tubes, and gas-meter, were exactly as used by Voit in his small respiration chamber, with the addition of an equipment for determining methane. Control experiments were made by burning candles in the apparatus. The authors claim that errors as large as 1 per cent in such determinations were very rarely found. With this combination of respiration chamber and tracheal canula, the investigators were able to compare the results obtained in short periods with those secured in 24-hour periods, and to check up the accuracy of their determinations obtained by using the tracheal canula.

*Stohmann, 1876.*[a]—In connection with a detailed account of his method of determining water-vapor in expired air, Stohmann describes briefly the respiration chamber used by him at Leipzig for large domestic animals. The chamber was constructed on the Pettenkofer principle, had a capacity of 15 cubic meters, and with it determinations could be made directly of the carbon-dioxide production. The chamber differed from the original Pettenkofer model in that the pumps were replaced by a "Roots silent blower." To regulate the ventilation there was inserted between the ventilator and the large gas-meter a three-forked tube, one fork of which connected with the ventilator, one with the gas-meter, while the third (regulated by a valve) led into the open air. The degree to which this valve was open or closed regulated the rate of ventilation. With the valve completely closed there was a ventilation of 150 cubic meters per hour; partially closed, the ventilation could be held at any desired rate down to as low as 10 cubic meters per hour. Although Stohmann stated that he would give a more complete description of this apparatus in another publication, we have been unable to find any later reference. He likewise speaks, on the first page of his article, of having constructed a respiration apparatus at the agricultural experiment station at Halle in 1870, but gives no reference to place of publication of the description of this apparatus.[b]

*Soxhlet, 1878.*—At the Agricultural Experiment Station in Vienna, in connection with some feeding experiments with steer calves in 1874 and 1875, Soxhlet carried out three 24-hour respiration experiments, two with a 65-kg. calf 14 to 23 days old and one with a 48-kg. calf 8 days old. Unfortunately, in the only reference[c] available to us, Soxhlet gives no description of his respiration chamber other than to state that it was a large one. His chamber was

[a] Stohmann, Landw. Versuchs-Stationen, 1876, 19, p. 81.

[b] We are much indebted to Professor Dr. E. Abderhalden, of Halle, Germany, for his efforts to locate the original Halle apparatus mentioned by Stohmann. Professor Abderhalden, in a personal communication, states that at the present date there is no respiration chamber for large animals at Halle, and he thinks that probably the Halle chamber must have been transported to Leipzig at the time of Stohmann's change of posts.

[c] Soxhlet, Erster Bericht ü. Arbeiten d. k. k. landw.-chem. Versuchsstation in Wien, Wien, 1878, p. 101.

not used again until several years later, when Meissl and Bersch carried out experiments with swine in this same apparatus. According to the description given by Meissl and Bersch,[a] the chamber was constructed on the Pettenkofer principle, had a capacity of 22 cubic meters, and could be ventilated at the rate of 50 cubic meters per hour. The apparatus is still in existence at the Agricultural Experiment Station in Vienna, but has not been used since Meissl and Bersch did their work with it.[b]

*Chauveau, 1892-93.*—A replica of the Pettenkofer-Voit respiration chamber of a size suitable for large animals was installed by Chauveau at the École Nationale Vétérinaire at Lyons about 1892 or 1893, but has never been used to study the metabolism of large animals and has not been described by Chauveau himself.[c] Tissot,[d] in 1902, employed this apparatus to study the effect of low atmospheric pressure upon the respiratory exchange of humans, and in reporting his results briefly describes the apparatus as a rectangular chamber of strong sheet-iron, 15 cubic meters in capacity.

*Kühn, Kellner et al., 1894.*[e]—A respiration chamber for large animals was built in 1880 at the experiment station at Möckern, Leipzig, based on the Pettenkofer apparatus in Munich, but embodying the modifications developed at the Weende-Göttingen station and other improvements developed by Kühn himself. With the Möckern chamber it was possible to determine only the carbon-dioxide production and marsh-gas and not, as with the Göttingen apparatus, the moisture in expired air. The chamber was constructed of strong sheet-iron and had a content of 18.21 cubic meters. A large number of control experiments were made with burning candles, giving most satisfactory results. Within the chamber was a manger for food and water, which could be closed air-tight from the outside. The feces were collected in a box in the floor, which also could be closed air-tight and the feces then removed. The urine was collected outside the chamber in a large flask connected with the bottom of the chamber by a tube, connected in turn with a urine funnel attached to the animal. The results of experiments carried out with this apparatus were made extensive use of by Kellner, director of the experiment station at Möckern, in his classic volume on animal nutrition.[f]

*Tangl, 1903.*[g]—A respiration chamber for large animals was constructed by Tangl in Budapest in 1903, but no experiments were carried out with it and no description of it has been published. After the first preliminary tests, such difficulties arose that the use of the apparatus was finally given up and the apparatus has remained untouched since that time.

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[a] Meissl and Bersch, Zeitschr. f. d. landw. Versuchswesen in Oesterreich, 1901, 4, p. 805.

[b] For the information regarding Soxhlet's chamber we are indebted to Professor Arnold Durig of Vienna, Austria, who kindly looked up the references unavailable to us and who communicated with the Vienna Agricultural Experiment Station for verification of the above statements.

[c] Information given by Professor F. Maignon (present director of the physiological laboratory of the École Nationale Vétérinaire at Lyons), in a personal communication, December 25, 1921.

[d] Tissot, Compt. rend. soc. de biol., 1902, 54, p. 682.

[e] Kühn, Thomas, Martin, Lankisch, König, Mohr, Böttcher, Koch, Waage, Mielcke, Köhler, Lösche, and Gerhard, Landw. Versuchs-Stationen, 1894, 44, p. 257. (Arbeiten d. kgl. landw. Versuchs-Station zu Möckern aus d. Jahren 1874–92, Berlin, 1894.)

[f] Kellner, Ernährung der landw. Nutztiere, 9th ed., Berlin, 1920.

[g] Information received in a personal communication from Professor Paul Hári, December 27, 1921.

*Zuntz, 1909-10.*[a]—At the Tierphysiologisches Institut of the Landwirtschaftliche Hochschule in Berlin, a respiration chamber of about 80 cubic meters capacity was constructed by Zuntz for studying horses and cattle. Within the chamber a treadmill was installed and likewise the tracheal canula equipment. This chamber could be used according to the modified Tigerstedt-Pettenkofer method. In this case a 500-liter gas-meter, actuated by an electric motor, secured ventilation of the chamber by the Pettenkofer principle, and the carbon dioxide was determined with the Pettersson apparatus, as modified by Tigerstedt and Sondén. Usually, however, the Regnault-Reiset method was employed, whereby the investigators were able to determine directly the carbon-dioxide production, oxygen consumption, and water-vapor. Oxygen was introduced into the chamber, as consumed, from a weighed cylinder of the gas.

A rotating blast-apparatus circulated 600 cubic meters of air per hour through the absorption apparatus for carbon dioxide and water-vapor. This consisted of a cylinder 7 meters high, in which the air came in contact with a system of cooling-tubes and was cooled to not far from $-10°$ C. A stream of potassium-hydroxide solution, falling constantly over the cooling-tubes, absorbed the carbon dioxide and the water-vapor so completely that the air of the respiration chamber, with a full-grown steer in it, never contained more than 0.07 per cent carbon dioxide and 6 mm. water-tension. The carbon dioxide absorbed in the stream of alkali was subsequently measured in an aliquot. Methane was determined in a special Pettersson electric combustion apparatus. A small opening in one side of the chamber allowed a man to enter, and platforms on both sides of the treadmill permitted him to get at all parts of the apparatus. The error thus introduced by the man's breathing within the chamber was corrected for mathematically, based on data secured by the investigators with man, or the man often wore a respiratory mask and bag, resembling a diver's outfit. In the construction of his apparatus, Zuntz provided for the possibility of later using it as a calorimeter by protection against heat-loss from the outside, following the example of Atwater and his colleagues. By measuring the temperature and quantity of the incoming and outgoing air he planned to determine the heat produced by the animal. The published control experiments certify to the extraordinary ingenuity of Professor Zuntz, whose indefatigability and genius alone made the design and completion of this apparatus possible.

*Armsby, 1903-1911.*[b]—In 1898, work was begun by Professor Henry Prentiss Armsby, at the Institute of Animal Nutrition, State College, Pennsylvania, upon the construction of a respiration calorimeter for farm animals, but it was not until 1902 that the preliminary tests of the apparatus were completed and the first actual experimental work begun. His apparatus is a modification of the respiration calorimeter originally installed at Wesleyan University,

[a] Zuntz, Landw. Jahrb., 1909, **38**, Erg.-Bd. 5, p. 473; also Zuntz, VIII. Internat. Physiol. Kongress, Wien, Sept. 1910. For further details see also Zuntz, Jahrb. d. deutsch. Landw.-Gesellschaft, 1912, 27, p. 180, and Umschau, No. 5, Jan. 1911; also Zuntz, Von der Heide, and Klein, Landw. Versuchs-Stationen, 1913, **79**, **80**, p. 806; *ibid.*, Landw. Jahrb., 1913, **44**, pp. 776 et seq.

[b] Armsby, Expt. Sta. Record, 1903–04, **15**, p. 1037; Armsby and Fries, U. S. Dept. Agric. Bur. Anim. Indus. Bull. 51, 1903, p. 23; Armsby, Agric. Expt. Sta., Pennsylvania State College, Bull. 104, 1910.

Middletown, Connecticut.[a] The respiration part of the apparatus is, in principle, a Pettenkofer apparatus. The ventilation is maintained by means of a large meter-pump at the rate of about 700 liters per minute. Samples of both ingoing and outcoming air pass through U-tubes containing sulphuric acid and soda-lime, by means of which carbon dioxide and water-vapor are measured. A sample of outcoming air is likewise passed over platinized kaolin maintained at a red heat and then through a second set of absorption tubes, for the purpose of determining the carbon and hydrogen of any combustible gases excreted by the animal. The chamber is also provided with calorimetric features. Through a series of copper pipes at the top of the chamber a uniform current of cold water is constantly circulated. The temperature of this water on entering and leaving is read every 4 minutes by calibrated mercurial thermometers reading to 0.01° C., and the volume of water passing through is measured in copper vessels holding 100 liters each. From these data the amount of heat brought out by the water current is readily computed. The walls of the chamber are double, the inner one being of sheet-copper and the outer of sheet-zinc, with a dead-space between. This metal chamber is surrounded by two double wooden walls inclosing spaces of about 10 cm. between the outer zinc surface of the chamber proper and the first wooden wall and between the latter and the second wooden wall, respectively. An adiabatic arrangement of thermo-electric couples, water-jackets, and electric heating-coils prevents loss of heat by radiation through the walls of the apparatus or in the air current, and the total amount of heat evolved by the animal is represented by the heat carried off in the water current plus the latent heat of vaporization of the water removed in the air current.

*Hagemann, 1911.*[b]—In addition to the instrument of Professor Armsby at State College, Pennsylvania, we know of but one other respiration calorimeter for large animals, namely, that used by Hagemann in Bonn. His calorimeter, which was copied in large part after Professor Armsby's, consists of three double-walled chambers, one within the other, the two outer ones constructed of wood and the innermost one of copper and zinc. The innermost chamber has a capacity of about 34 cubic meters. Hagemann has reported experiments with two steers and one horse. A correction of considerable size is necessary, not only in the determination of heat, but even in the measurement of carbon dioxide.

*Møllgaard and Andersen, 1917.*[c]—At the Veterinary High School in Copenhagen, a remarkably complete respiration chamber of 13.13 cubic meters capacity, embodying the Pettenkofer principle and the Jaquet principle for oxygen, has been constructed within the last five years by Møllgaard and Andersen. With this chamber direct determinations have been made of the carbon-dioxide production, oxygen consumption, and methane production of milch cows.

*Hill, 1914,*[d] *and Capstick, 1921.*[e]—A self-recording calorimeter for large animals, constructed at the Cambridge School of Agriculture, England,

[a] Atwater and Rosa, U. S. Dept. Agric., Office Expt. Sta. Bull. 63, 1899; also Atwater and Benedict, U. S. Dept. Agric., Office Expt. Sta. Bull. 136, 1903.

[b] Hagemann, Landw. Jahrb., 1911, 41, Erg.-Bd. 1, pp. 1 et seq.

[c] Møllgaard and Andersen, Kgl. Veterinaer-og Landbohøjskole Aarsskrift, Copenhagen, 1917, p. 195.

[d] Hill, A. V., and Hill, A. M., Journ. Physiol., 1914, 48, p. xiii.

[e] Capstick, Journ. Agric. Sci., 1921, 11, p. 408.

was briefly described in 1914 by A. V. and A. M. Hill, and has recently been described in greater detail by Capstick. The body of the calorimeter consists of a cylindrical galvanized-iron tank, 9½ feet long and 5½ feet in diameter. A ¾-inch lead pipe is soldered in a helix around the outside of the cylindrical part of the tank and in a spiral over one end, while a door covers the other end. Water, maintained at a constant temperature by a thermostat, circulates through the lead pipe and finally through 80 feet of ½-inch tube near the roof of the tank. The quantity of heat given off by an animal is calculated in the usual way from the rate of flow of the water and the difference of temperature between the inlet and outlet water, with suitable corrections which are mentioned in Capstick's paper. No arrangement for measuring the products of respiration is described, and the calorimeter is not large enough for a full-grown steer. Capstick reports that in its present state the calorimeter will, under favorable circumstances, give fairly accurate results, but it is not to be regarded as other than an experimental piece of apparatus. The extraordinary agreement in control experiments, as reported, suggests that Capstick's claims are too modest.

## RESPIRATION APPARATUS USED IN THE RESEARCH.

### Simplified, Practical Respiration Apparatus Needed.

In recent years, therefore, we have seen the construction of four notable pieces of apparatus that far exceed in complexity the original Pettenkofer-Voit apparatus, namely, that of Zuntz in Berlin, that of Møllgaard and Andersen in Copenhagen, and finally, that of Armsby at State College, Pennsylvania, subsequently copied in Bonn. A large part of the complexity of the Armsby apparatus was necessitated by the fact that he alone, of all the investigators thus far cited, attempted and succeeded in measuring the direct heat-production of large domestic animals. It is obvious that the initial expense of construction and installation, the cost of maintenance, and the experimental staff needed for the successful conduct of experiments with the older and more complicated form of apparatus generally preclude a wide application of studies of respiratory exchange to animal feeding. Thus, for example, in America, where agricultural research has always received great attention, until 1918 (when the Durham chamber was constructed), but one respiration apparatus for large domestic animals existed, and that was Professor H. P. Armsby's at State College, Pennsylvania.

The necessity of extensive food regulations and readjustments of distribution as a result of the Great War, and particularly the necessity for making usable for man some of the foods formerly given to animals, stimulated further research upon the energy expenditure and economy in the nutrition of farm animals. While the Nutrition Laboratory had successfully installed a large respiration chamber, indeed sufficiently large for successful experiments with a group of 25 young women,[a] no attempts had until that time been made to utilize this principle for studying the respiratory exchange of the larger domestic animals. It seemed an opportune moment to construct a respiration chamber on this simplified principle for animals, and consequently, after the affiliation with the New Hampshire Agricultural Experiment Station, a res-

[a] Benedict and Johnson, Proc. Am. Philos. Soc., 1919, 58, p. 89.

piration chamber with its appurtenances was constructed by the mechanical department of the Nutrition Laboratory, shipped to Durham, New Hampshire, reassembled, and put into immediate operation. In the following description of the respiration apparatus attention should be especially directed to the fact that every attempt was made to minimize expense. Indeed, permanency of construction was in part sacrificed to expediency in the demand for quick results, and since at that time we were dealing with enormously inflated prices, the selection of material was frequently made solely to minimize expense. In the description which follows occasional recommendations will be made, based upon an intensive 5-years' use of this apparatus, recommendations which would be followed by us in case the apparatus were to be rebuilt.

A personal inspection of most of the earlier respiration apparatus showed either a respiration chamber constructed of riveted boiler-plate iron or (as in the case of the respiration calorimeter of Professor Armsby at State College, Pennsylvania, and its replica at Bonn) an extraordinarily intricate wall construction with polished copper, etc. In both of these latter cases, however, this construction was predetermined by the desire for heat measurements. Their complication in construction together with their correspondingly large staff of operators preclude their use under any but the most restricted conditions. No reasonable expectation of their general usage by experiment stations may at present be entertained.

Our prime object was to have available a respiration apparatus for animals that, in the first place, would be accurate, second, would be relatively inexpensive to construct and install, and third, would not require an extensive staff for its successful operation. We had the advantage of the two years' experience of the Nutrition Laboratory with the large respiration chamber and its accessory features, from which the new chamber was ultimately in large part copied. Consequently, in the construction of this apparatus expensive fixtures are conspicuous by their absence. Thus, we find no highly polished copper walls, no boiler-plate iron, no nickel-plated fittings and polished woodwork, but every aesthetic point was sacrificed to secure an apparatus of rigid, reasonably permanent construction, which under all circumstances must at least be perfectly accurate.

While the earlier respiration apparatus, particularly those on the Pettenkofer-Voit principle, were confined solely to estimations of carbon dioxide and methane, the more recent apparatus, namely, those of Zuntz and Møllgaard and Andersen, very properly include measurements of oxygen as well as carbon dioxide. In planning the construction of the new apparatus, the proportionate values of carbon-dioxide determinations and oxygen determinations need special consideration. Technically, the determination of carbon dioxide is much easier than that of oxygen. Physiologically the measurement of oxygen is a much more accurate and immediate measure of the simultaneous energy transformations than is the measurement of the carbon-dioxide output. An examination of the present situation with regard to the oxygen determination of large animals shows that but two of the apparatus provide for this in their published descriptions, that of Professor Zuntz and that of Møllgaard and Andersen, although Professor Armsby informed us that for the past two years this has been successfully accomplished with his apparatus at State College.

Finally, in considering the factors that should reasonably be measured by an apparatus for which relatively wide distribution might be expected, we were much influenced by the large amount of scientific data of most fundamental importance already secured by the decade of experimenting by Professor Armsby, which seemed to imply a reasonable uniformity between carbon-dioxide measurement and direct heat-production. It thus appeared for the first time that the carbon-dioxide measurement alone might now have much greater significance than during the earlier days when accompanying heat measurements had not been accomplished. Professor Armsby and his associates were good enough to recompute many of their data to establish the relationship between carbon dioxide and heat-production, and came to the final conclusion that "by the use of this ratio the heat production may be computed from the observed $CO_2$ production with a good degree of accuracy, at least for animals on dry feed and not performing work."[a] Hence, as a matter of pure expediency, the Durham apparatus was primarily constructed for the determination of carbon dioxide only.

The large respiration chamber used in the Nutrition Laboratory had been made solely for the measurement of carbon dioxide. The absence of a large ballast or fill, with its fermentations or prolonged digestion, made it possible in the case of man to estimate with reasonable exactness the probable calorific value of carbon dioxide under the conditions of experimentation. With ruminants this problem was greatly complicated. Still, again basing all of our advances in the accuracy and particularly the interpretation of the measurements of carbon dioxide upon the classic and fundamental researches of Professor Armsby, we are at the present date in a position to use carbon-dioxide measurements for the interpretation of metabolic processes with a far greater probability of correctness than was possible with the earlier types of apparatus. While, therefore, we are in no sense disposed to minimize the advisability and great desirability of simultaneous measurements of carbon-dioxide production, oxygen consumption, methane elimination, and particularly direct heat measurements, we have come to the conclusion, based upon Professor Armsby's remarkable contributions to the gaseous metabolism of animals, that an apparatus which measures accurately, rapidly and inexpensively carbon-dioxide production, has a proper field in experiment station researches.

### General Principle of the Respiration Apparatus.

One of the first essentials is, of course, an air-tight respiration chamber, which can be ventilated with pure, uncontaminated outdoor air. The carbon dioxide produced by the animal inside the chamber must be either measured *in toto* or a definite aliquot of the total ventilation must be obtained and the carbon dioxide in it measured. In our apparatus, an electric blower drives pure, outdoor air into the chamber. A second blower inside the chamber discharges air from the chamber out through the wall into a small wind chest provided with two circular openings, the areas of which are such as to allow approximately 90 per cent of the air to be discharged into the room or laboratory and 10 per cent into a superimposed metal can pro-

[a] Armsby, Fries, and Braman, Proc. Nat. Acad. Sci., 1920, 6, p. 265.

vided with a light-weight rubber bathing-cap cover. This last fraction of the air, i. e., 10 per cent, is the aliquot from which ultimately the carbon dioxide is absorbed. The air discharged into this sampling-can is continuously withdrawn by a positive blower and forced through sulphuric acid, where water is quantitatively absorbed, and then through soda-lime, where the carbon dioxide is quantitatively absorbed. Since experience has shown that the soda-lime best absorbs carbon dioxide when slightly moist, it obviously gives up water-vapor to the previously dried air current coming from the sulphuric-acid vessel, and consequently it is necessary to absorb the water-vapor taken up from the soda-lime by passing the air current through a second vessel containing sulphuric acid.

Outdoor air contains a small, though very constant (0.03 per cent), amount of carbon dioxide. To allow for this the total volume of the air passing through the sulphuric-acid and soda-lime containers must be known, and consequently the air leaving these absorbing vessels is passed through a dry gas-meter. In order to make observations upon the animal at repeated intervals and, indeed, to continue experiments over a long time, it is desirable to change the absorbing vessels from time to time. This is done by deflecting the air current from the sampling can alternately through two separate sets of purifiers by simultaneously turning suitable valves. Under these conditions experiments can be carried on as long as desired and in periods as short as, in actual practice, 20 to 30 minutes.

The general principle of the respiration apparatus and the relations of its several parts are shown in Fig. 6. Here it can be seen that the apparatus consists of two separate, main parts: first, the respiration chamber itself; second, the ventilating appliances, which include the aliquoting chamber or wind chest and a double system of purifying vessels for quantitatively absorbing water-vapor and carbon dioxide.

### Description of Respiration Chamber.

In designing the respiration chamber two important facts had to be kept in mind: first, the chamber must be absolutely air-tight; second, it must have an opening or door sufficiently large to admit a full-grown steer and yet so constructed that it can be satisfactorily closed in order to eliminate the disastrous effects of the leakage of room air of unknown composition into the chamber or a leakage of air from the chamber. Theoretically, almost any form of air-tight chamber could be used. Technically, the smallest volume of extraneous air about the animal inside the chamber permits of the most accurate measurements—that is, the smaller the volume of extraneous air, the less the necessity for correction for changes in the composition of residual air in the chamber at the end of any given period. Since at all times the pressure inside the respiration chamber was to be atmospheric, the rigid, expensive, boiler-plate construction of many of the earlier chambers seemed entirely unnecessary, and an air-tight sheet-metal shell, reenforced on the inside by a rugged framework to withstand the lunges of a heavy steer, was deemed sufficient to meet all experimental conditions and at a greatly reduced cost. Consequently, a rugged wooden framework was first constructed, to which could be attached the stanchions, the platform upon which the steer would stand, and all the other appliances inside the chamber.

Around this rugged wooden framework a reasonably light sheet-metal wall was constructed. While our original design was rectangular, a wedge-shaped construction with the smaller end at the head could perfectly well be used, and thus reduce perceptibly the inner air volume. Under all considerations, however, it is necessary to insure that the animal can not, either with hoofs or side or horns, touch the light sheet-metal, which could easily

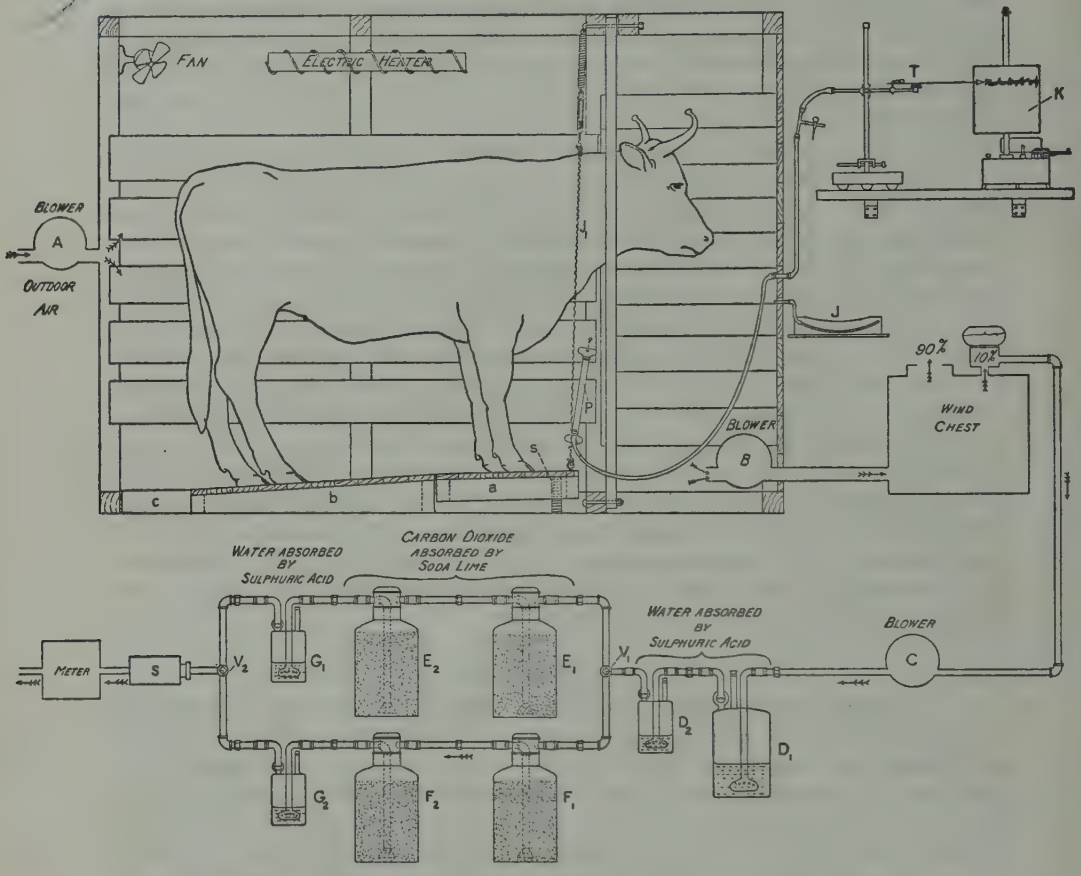


FIG. 6.—Detailed scheme of respiration chamber, aliquoting chamber or wind chest, and absorbing system, for determing the respiratory exchange of large domestic animals.

Pure outdoor air is introduced into chamber by blower *A*, is withdrawn by blower *B*, and forced into wind-chest. Through one of two circular openings in wind-chest 90 per cent of air escapes into room; 10 per cent passes into sampling-can with rubber bathing-cap top. Blower *C* forces air withdrawn from sampling can through two sulphuric-acid bottles, $D_1$ and $D_2$. Valve $V_1$ deflects air through either one of two sets of soda-lime bottles, $E_1$ and $E_2$ or $F_1$ and $F_2$, and sulphuric-acid bottles, $G_1$ or $G_2$. Air then passes from sodium-bicarbonate container *S* through meter. Delicate petroleum manometer *J* is used to indicate pressure inside chamber. To register muscular activity of animal floor is in two sections; at front a movable platform, *a*, supported by two chains attached to springs at top of chamber and by two compression springs resting on the metal floor of chamber, only one of which, *s*, is shown. Rear of floor is a fixed platform, *b*, slanting to allow flow of urine into container, *c*. *P*, pneumograph attached at one end to one of the chains, $j_1$, supporting movable platform, *a*, and at the other end to one of the stall uprights. Changes in tension of air in pneumograph transmitted through rubber tubing with safety outlet and pinchcock to tambour *T*, which actuates a small pointer writing on kymograph drum *K*.

be perforated, thus producing a leak. In the construction of the chamber, therefore, we have two essentially different parts: first, the wooden framework, stanchions, and platform; second, the outer, air-tight wall-covering of sheet-metal. Part of the construction, the wooden framework, is already indicated in Fig. 6 (p. 50), showing the uprights, position of stanchions, and the board protection in the head end of the chamber to prevent the horns of the steer from coming in contact directly with the sheet-metal.

As finally constructed, this respiration chamber measures 7 by 9.6 by 5.4 feet (2.1 by 2.9 by 1.6 meters) and has a capacity of approximately 9,000 liters.

For purposes of transportation a frame that could be more or less "knocked-down" was necessary, since this entire apparatus was constructed at the Nutrition Laboratory in Boston, loaded upon a motor truck, and transported 60 miles over the roads to the Agricultural Experiment Station at Durham. The outside shell was for similar reasons made in several sections, with well locked and soldered seams, and finally assembled in Durham after the framework had been mounted. We see, therefore, no particular reason why this same principle should not be applied in any new construction. For this purpose, the two rectangular frames at the front and the rear of the chamber were first constructed. The front consists simply of four pieces of 4 by 4 inch spruce, joined together either with spikes or angle irons, the ends being halved, as shown in Fig. 7. The rear is similarly constructed, except that the two uprights, instead of being 4 by 4 inches are 3 by 8 inches, thus providing for the door frame and for extra reenforcement in case an animal should hit the sides in entering or leaving. These two end frames are connected at the corners by a series of four 4 by 4 inch stringers, joined to the front and rear frames by angle irons. (See Fig. 7.) Finally, to support the stanchions and serve as extra reenforcement, 4 by 4 inch cross pieces (see *g*, *g*, *g*,*g*, Fig. 7) are provided, one at the bottom to support the base of the stanchions, two at the top for both sides of the stanchions, and one at the top half way between the rear of the chamber and the stanchions. Extra upright 4 by 4 inch pieces are also inserted on both sides opposite the extra cross pieces just mentioned.

As can be seen in Fig. 7, most of the joints are made with 4-inch angle irons, *e*, screwed to the 4-inch woodwork with suitable-sized lag-screws. Two upright planks, $f_1$ and $f_2$ (Figs. 7, 9, and 10), provide the stanchions, $f_1$ being rigidly fixed, and $f_2$ having the top loose so as to slide back and forth between the two cross members *g* and *g* (Figs. 7 and 10), ultimately held in position by a long bolt kept in place by a wooden button (*x*, Figs. 7 and 10), so the head can not slip out. This makes the whole framework very rigid. Indeed, even with the heaviest steers, we have found it sufficiently rugged to withstand all the lunges and activity produced by them. Several coats of paint prevent undue shrinking or warping.

To prevent the animal from touching the metal walls on the sides, extra planks are spiked to the 4 by 4 inch uprights, and by providing extra supports along the cross-members *g* and *g* (Figs. 7 and 10) from top to bottom, the stall can be narrowed to give even less activity to the animal in the forward part of the chamber. As stated before, the chamber can be made entirely wedge-shaped, if desired, and thus perceptibly narrowed. Since this chamber

has been used, however, not simply for steers but has been pretty well packed with sheep, we have found the present volume to be very suitable and adaptable.

Deferring for the time being the discussion of the special flooring, the construction of which is determined by the desire to secure graphic records of activity of the animal, we may pass to the sheet-metal shell. Owing to the prohibitive cost of copper at the time this apparatus was constructed,

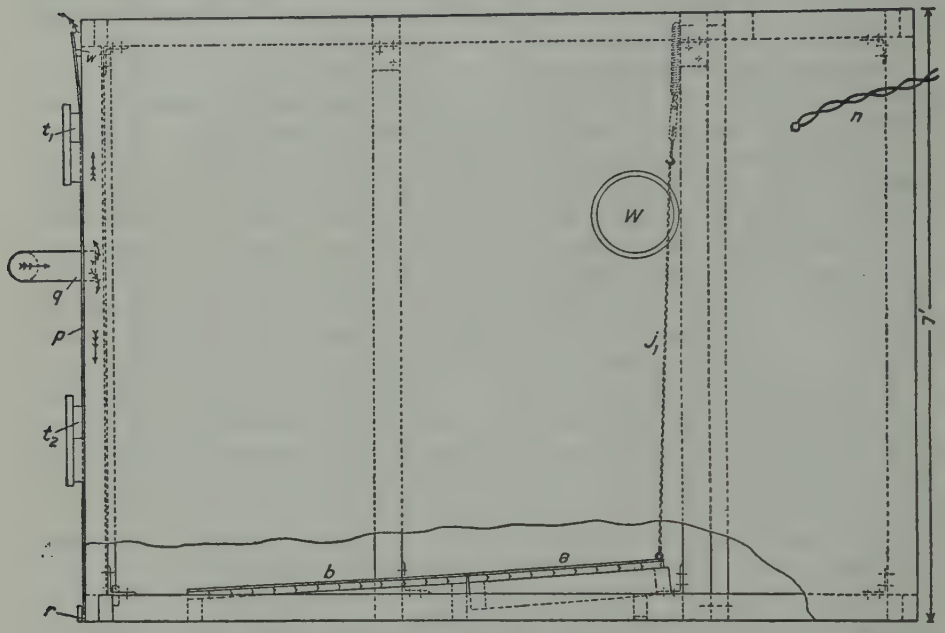


FIG. 8.—View of side elevation of respiration chamber.

Side elevation shows front movable platform *a;* rear, fixed platform *b;* chain $j_1$, attached to front platform *a;* pipe *q* from blower, delivering outdoor air into space between door panels; recessed wooden strip *r*, and cross-bars $t_1$ and $t_2$, dropped in sockets on outer metal wall, to hold outer door panel *p*, in place; one of two wooden wedges, *w*, to adjust closure of outer door panel *p;* electric leads *n*, for lights, heaters, fans, and blower inside chamber; *W*, window. (See Fig. 9 for floor plan.)

we had to use galvanized iron. Copper is recommended for two reasons: first, it does not rust, and second, it is much easier to manipulate, handle, and solder. The walls and top of this chamber were No. 28 gage (0.020 inch) galvanized sheet-iron, and since more wear and tear comes upon the floor, with the possibility of urine rusting it out earlier, a heavier gage, No. 24 (0.028-inch) was used for the bottom. The bottom was then thoroughly painted on the inside with an asphalt paint to aid further in its rust-resisting properties. If urine is to get upon the floor (and with sheep experiments this is unavoidable), it is highly desirable to have the construction such that there will not be an opportunity for liquid to accumulate between the woodwork and the sheet metal. Hence we would recommend an inner flashing of sheet metal to connect with the floor on the inside, cover the 4 by 4 inch

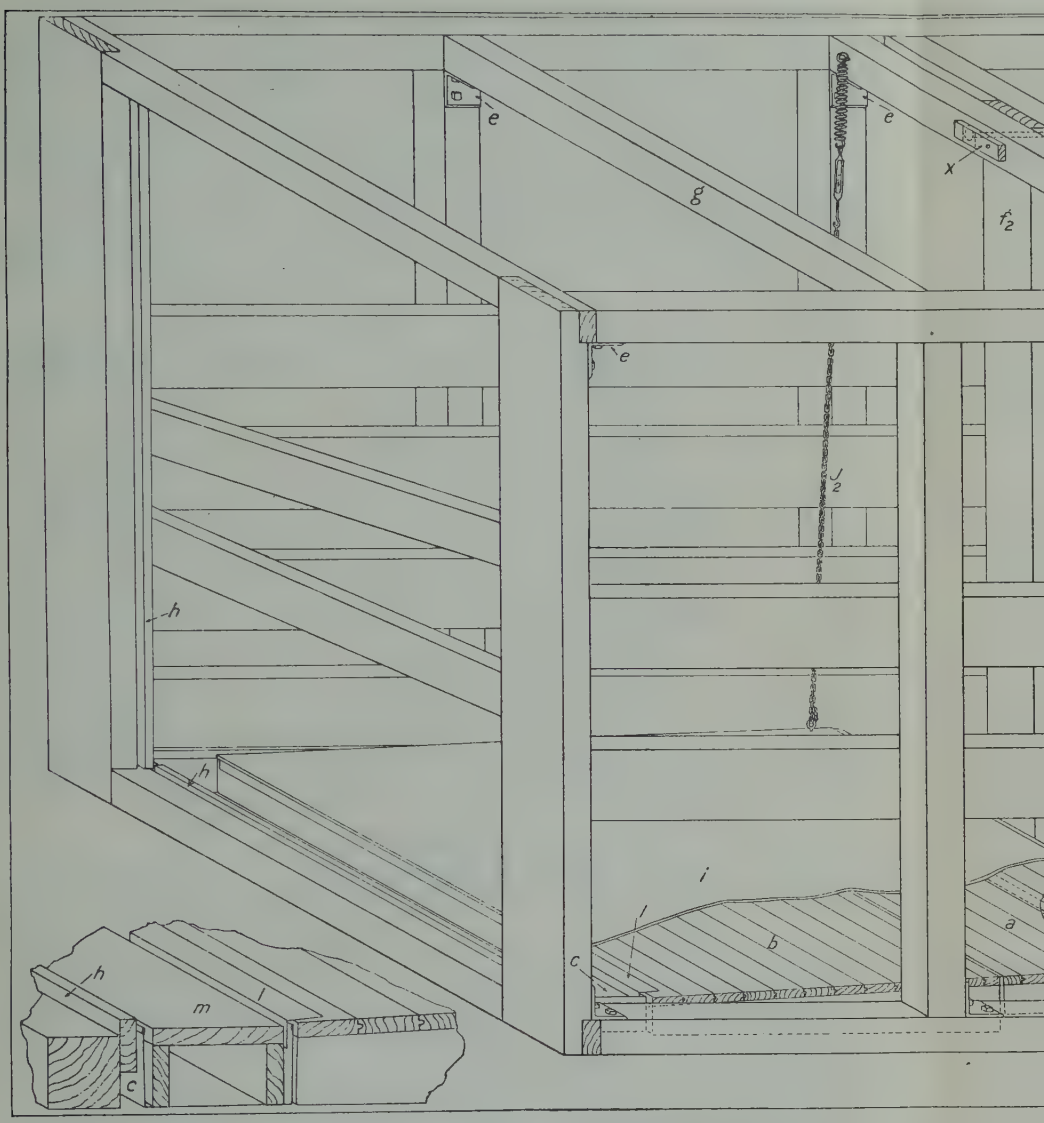


FIG. 7.—Isometric perspective of respiration chamber for large domestic animals

A sheet-metal shell with locked seams *d*, soldered to insure air-tight closure, is built over a wooden f square, spiked together and reenforced by 4-inch angle irons *e*, attached by lag-screws. Stanchions $f_1$ an from coming in contact with metal walls by 2-inch planks spiked on the inside of the uprights. Door fra two sections covered with linoleum *i*. Front of floor a movable platform *a*, under which are two com one of which, *s*, is shown. Compresssion springs fastened to flat iron bar *y*. Two chains, $j_1$ and $j_2$, are from cross-member *g*. Rear of floor a fixed platform *b*, which slants to allow flow of urine and feces into c iron *l*, bent at right angles, one side resting over edge of container *c*, and the other side under edge of linc Electric leads *n* are for lights, heaters, fans, and blower inside chamber.

woodwork around the bottom edge, and extend up on the sides sufficiently to prevent accumulation of liquid.

Owing to the size of the room available at Durham, it was necessary to place the chamber directly upon the concrete floor of the barn. We recommend that it be elevated a foot or two, if space for a runway leading into the chamber is available. This would make it possible to put an opening in the bottom of the chamber, and flush it with water. The elevation of the chamber does, however, necessitate more rigid reenforcement and bracing, particularly at the top, to prevent possible damage from vigorous movements of an active steer. Finally, it would be highly desirable to have the whole chamber slightly elevated at the front end, so as to have all urine spilling upon the floor naturally settle at the rear.

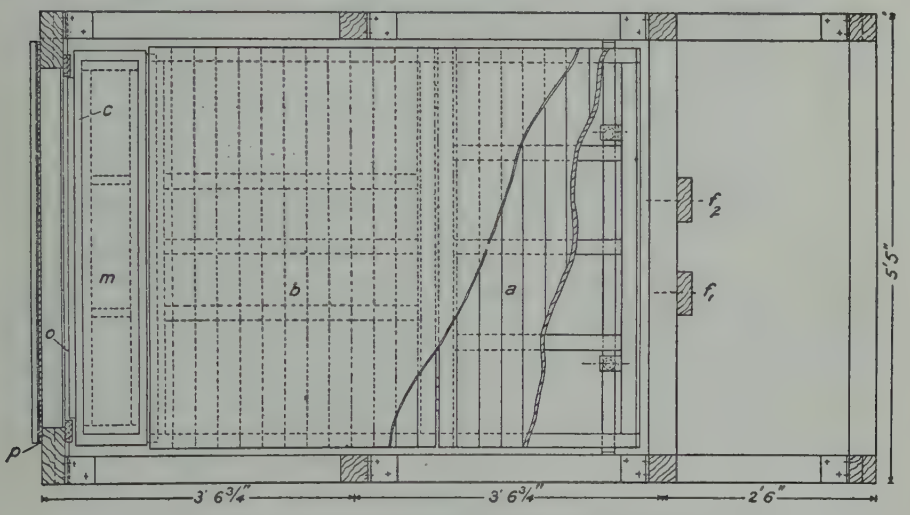


FIG. 9.—View of floor plan of respiration chamber.

Floor plan shows location of front movable platform *a*; rear fixed platform *b*, stanchions $f_1$ and $f_2$; urine receptacle *c*; oak platform, *m*, to prevent animal from stepping into urine receptacle; and inner and outer door panels, *o* and *p*, in place.

*Constructional drawings.*—Primarily for the purpose of assisting in the possible reconstruction of this apparatus, four scale drawings were prepared, giving the side elevation, floor plan, front and rear elevations. (See Figs. 8 to 11.) In most instances they are lettered in accordance with the main lettering on Figs. 6 and 7, and examination of these two latter figures will easily locate any individual parts with respect to the whole. Frequent reference will be made subsequently to these four figures in the discussion of the further equipment and use of the chamber. Dimensions are given in feet and inches.

*Openings in the wall of the chamber.*—The sheet-metal flashing is carried around the door-jamb *h* (Figs. 7 and 11) into the inside of the chamber. The window (*W*, Fig. 8) through which the animal may be observed is circular, 12 inches in diameter, and the circular disk of glass is permanently waxed into place in this opening. Small openings for ventilating air-pipes, tube to pneumograph, electric wires, etc., are easily obtained by soldering short lengths of small brass tubing of suitable size into the galvanized-iron wall.

FLOOR AND ARRANGEMENT FOR RECORD OF MUSCULAR ACTIVITY.

Extended experience with humans and other animals in the Nutrition Laboratory has shown the desirability of knowing with relative accuracy the degree of muscular repose during any measurement of gaseous metabolism. With these larger animals it was recognized at the start that minimum muscular repose could not be secured, for the animals lie down very irregularly, and hence the majority of the experiments were made in the standing position. Even when quietly standing, animals vary greatly in their degree of restlessness or repose. To render our metabolism measurements more intelligible, therefore, we devised an apparatus whereby we could register graphically the degree of activity of the animals. The details of this apparatus are shown in Figs. 6 and 7.

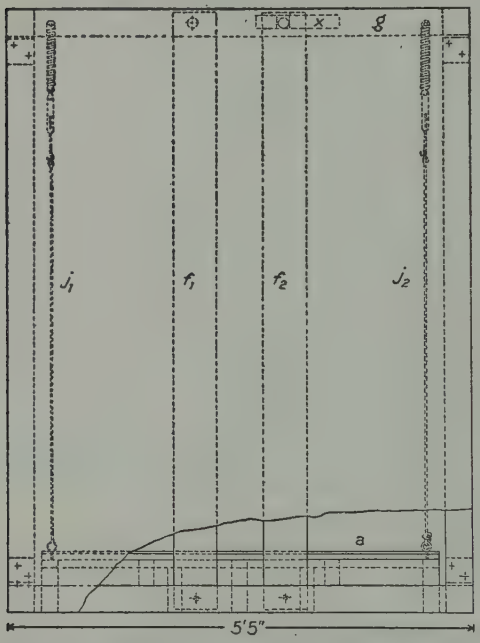


FIG. 10.—View of front elevation of respiration chamber.

Front elevation shows the two stanchions, $f_1$ and $f_2$, with button $x$, holding bolt in place for securing movable stanchion, $f_2$; the front, movable platform of floor $a$, supported by springs and chains $j_1$ and $j_2$, which in turn are attached to cross-member $g$. A loose chain (not shown in figure) is fastened between stanchions $f_1$ and $f_2$ under the animal's neck to prevent animal from lying down.

Recognizing the fact that practically any movement of the body results in a change in the center of gravity that is sufficient to alter materially the proportion of weight resting on the front and hind legs with animals, we have made the front part of the floor of the stall in the form of a movable or hinged platform $a$. The hind legs stand upon a fixed floor $b$, the front legs upon the movable platform $a$. This movable platform is supported by two chains, $j_1$ and $j_2$, which are attached to two springs hooked to the framework of the chamber, and by two compression springs $s$, resting on the metal floor of the chamber.[a] The slightest change in the center of gravity of the animal results

[a] The two compression springs $s$ are made of approximately ¼-inch steel wire, have an outside diameter of 1.5 inches, and are 6.5 inches full length. Both the upper and lower ends of the springs rest on centering spools, the lower spools being fastened to a flat iron bar $y$, each 12.5 inches from the ends of the bar. This iron bar $y$ is a piece of strap iron 1.75 inches wide, bent at right angles at each end, and extending across the metal floor of the chamber, being attached on the inside of the longitudinal floor-beams. (See Fig. 7.)

in change of tension on all these springs. To one of the chains supporting the movable platform $a$ is attached one end of a pneumograph[a] $P$, the other end of which is attached to one of the uprights. (See Fig. 6 for approximate location.) Changes in tension of the springs will produce changes in length of the pneumograph $P$, and, consequently, a slight change in the tension of the air inside the pneumograph. This change in tension of the air inside the pneumograph is transmitted through a small rubber

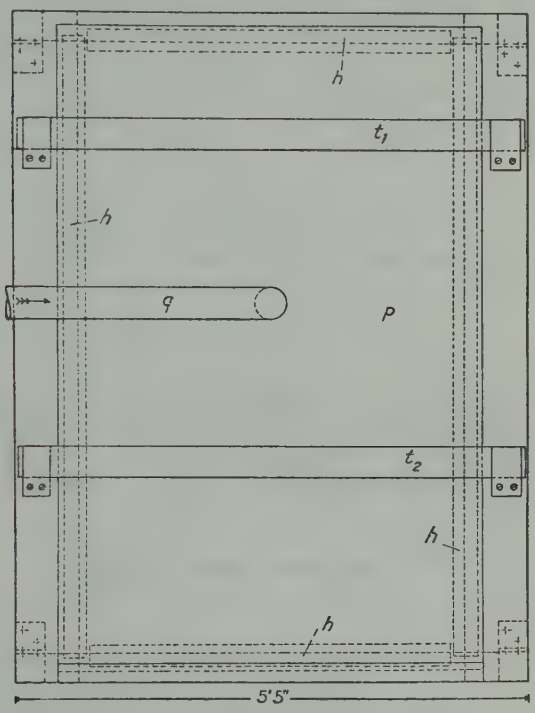


FIG. 11.—Rear elevation of respiration chamber.

Rear elevation shows air-pipe $q$, from blower delivering air into space between outer and inner door panels; the cross-bars $t_1$ and $t_2$, which are dropped into sockets on outer metal wall to hold outer door panel $p$ in place and door-jamb $h$.

diaphragm or tambour $T$, which in turn actuates a small pointer writing on the smoked paper of a clockwork kymograph drum, $K$.[b] If the animal stood perfectly still, the pointer obviously would record a straight line as the kymograph drum rotates. This disposition of the movable platform, pneumograph and connection with tambour is shown in detail in Fig. 6. While it is extremely difficult to ascribe any quantitative relationships to variations in the line drawn by the pointer on the kymograph drum, it is still very simple to compare the degrees of activity in two different periods and clearly state which period has the lesser degree of activity. Illustrations of typical kymograph records, secured with a steer relatively quiet and with another steer relatively active, are shown in Fig. 12 (p. 56).

[a] An inexpensive and satisfactory pneumograph is that furnished by the Harvard Apparatus Company of Dover, Massachusetts. It is approximately 15 inches long and consists of a thin-walled rubber tube, reenforced with a spiral spring, the two ends being closed with metal plates, one end having a small metal tube over which a rubber tube may be passed.

[b] A most satisfactory and relatively inexpensive kymograph is likewise furnished by the Harvard Apparatus Company of Dover, Massachusetts.

PROVISION FOR CARE OF EXCRETA.

The whole design of this apparatus was based upon its probable exclusive use in rather short, i. e., 2- or 3-hour respiration experiments. Consequently no particular provision for the continuous quantitative collection of urine and feces was provided. As a matter of fact, by very simple attachments we have succeeded in running 24-hour experiments successfully. The chief difficulty with the excreta, therefore, is the matter of contamination in the chamber, cleanliness, and particularly the difficulty of preventing the floor from rusting. To provide a proper receptacle for collecting in large part the urine

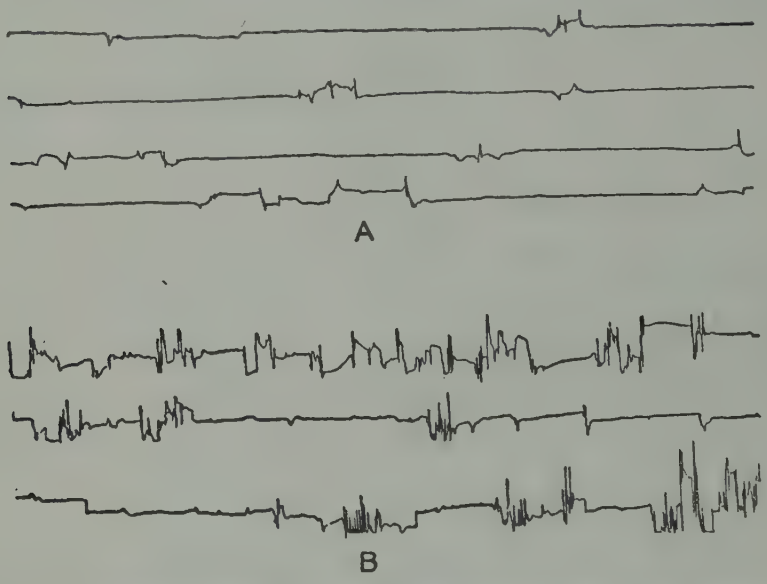


FIG. 12.—Portions of typical kymograph curves showing records of the muscular activity of steers studied in the respiration chamber.

The upper curve *A* is illustrative of relatively complete muscular repose; the lower curve *B* illustrates considerable activity.

and feces, the fixed and movable parts of the platform upon which the animal stands are covered with a continuous piece of heavy linoleum *i*, which extends from the front to the rear of the platform and there delivers urine into a long pan *c*, extending the entire width of the chamber. As both parts of the platform are provided with a slight slant toward the rear, the urine collection is thus reasonably complete. Certain details of this are shown in the enlarged portion of the lower left-hand part of Fig. 7. A small strip of galvanized iron *l*, bent at right angles, one side resting over the edge of the pan *c*, the other side under the edge of the linoleum *i*, makes the delivery of the urine more certain. Feces are in large part dropped into this pan. To prevent the animal stepping into the pan as it enters or leaves the chamber, a substantial oak platform *m* is set loosely into pan *c*, with its top flush with the top of the linoleum. This does not hinder the flow of urine into the pan and protects the pan perfectly. When quantitative urine collection is desired (as was the case in all experiments with steers A and B in the second

year's work) a urine funnel is attached to the steer, and the tube from the funnel is connected through an opening in the side wall with a discharge tube dipping 2 or 3 inches in a receptacle of water outside. If the respiration chamber were erected 18 to 24 inches above the floor of the building, this would facilitate greatly the matter of urine collection, and we see no reason why feces collection should not be made with equal accuracy, provided the pipe through which the feces are passed out through the wall of the chamber is water-sealed at its lower end. The fact that these seemingly crude arrangements for the collection of the major portion of the feces and urine have so protected the chamber that after 5 years' constant use the apparatus has still not perceptibly rusted and is perfectly air-tight, shows that the chamber has successfully accomplished its designed purpose. It still remains an obvious fact, however, that the substitution of heavy sheet copper for galvanized iron is to be recommended.

### INTRODUCTION OF FEED.

The apparatus was designed specially for short experiments, but if long periods of observation are desired, any one of the various types of feed chambers may be employed. Obviously, as can be seen from Figs. 6 and 7, plenty of space forward of the stanchions is available for this purpose.

### TEMPERATURE CONTROL.

The still unsettled question as to the influence of environmental temperature upon basal metabolism made it desirable to secure measurements at as uniform a temperature throughout the entire year as possible. The dairy barn was not artificially heated. Outside temperatures at times ranged very low, but the attempt was made to secure a reasonably uniform temperature by means of two electrical heaters, which were placed, as a matter of fact, near the head of the animal. (See Fig. 6.) That the two heaters here used were only partially successful is shown by the fact that, in spite of their use, the temperatures at which the respiration experiments were conducted varied greatly, indeed, so greatly as to make it necessary to indicate on many of the tables the exact temperature under which the measurement was made. It is obvious that only duplication of heaters is necessary to make this temperature control as nearly perfect as one desires. We were, frankly, negligent in this matter.

### VENTILATION OF THE RESPIRATION CHAMBER.

In order to determine the carbon-dioxide production of these large animals it is necessary that the chamber be ventilated with a known amount of pure, uncontaminated outdoor air, and in such an amount as to maintain the animal in a degree of comfort and keep the carbon-dioxide percentage sufficiently low so that the respiration will not be disturbed. Several years' experience with relatively high carbon-dioxide percentages in the atmospheric air has shown with men, at least, that until the percentage rises well above 1 no noticeable effects upon respiration occur and that a perfectly safe limit would be to keep the carbon dioxide in this respiration chamber about one per cent. Subsequently a careful series of analyses of the air in the Durham dairy barn[a] showed that the percentage of carbon dioxide is relatively high, i. e., 0.2 to

[a] Hendry and Johnson, Journ. Agric. Research, 1920, 20, p. 405.

0.3 per cent, so the animals are continually living in an atmosphere not far from this percentage. In practically all of our work the ventilation rate was so adjusted to the carbon-dioxide production of the animal as to have the carbon-dioxide content of the air inside the chamber somewhat less than one-half of 1 per cent. If the respiration chamber could be placed out of doors or in a perfectly ventilated room, where the air would have the composition of outdoor air, it would be possible to ventilate the chamber by having the air leak through a crack in the door, or, by putting in a pipe of certain length and size, air could be allowed to flow in and take the place of the air removed from the chamber by the ventilating blower.

Since it was impossible to build the chamber out of doors (indeed, it had to be built in a dairy barn with a relatively high percentage of carbon dioxide), the chamber had to be so constructed as to be free from leaks and so that only fresh, uncontaminated outdoor air could be introduced. The necessity for having the animal enter from the side precluded any possibility of a water seal, and, based upon the Nutrition Laboratory's experience of closing its calorimeter doors, our first thought was to seal in the door either with putty or with wax, and then pass the outdoor air through a suitable opening into the chamber. Before this laborious system was introduced, however, a most ingenious suggestion of Mr. Warren E. Collins (the former mechanician of the Nutrition Laboratory) was tried and has been found to work most satisfactorily. Mr. Collins's idea was that if the door was made of two parts with an air-space between, and if pure air could be supplied in excess to the air-space, then only pure air would leak into the chamber and the excess air would leak back from the air-space into the barn.

### Construction of Door.

In accordance with this plan, the door consists of two separate panels of ¼-inch "compo-board," each fitting into a recess in the framework. This composition board is very light, rigid, and practically air-tight. One of these panels, *o*, rests against a jamb, *h*, flush with the inside of the heavy door framework. (See Figs. 7, 8, 9, 11 and 13 for details.) This panel is held in place by a series of pins or nails (see *r*, Fig. 13) set loosely into suitable holes in the upright sides of the door-frame, so as to project an inch or more. Between the nails and the panel *o*, wooden wedges *w* are used to press the panel well into place, though no attempt is made to have the closure strictly air-tight. A second compo-board panel,[a] *p*, slightly larger, is then placed over the opening on the outside of the sheet-metal wall, thus allowing about a 3-inch air-space between the two panels. The bottom edge of the outer panel, *p*, rests on a recessed wooden strip to assist in holding it in place. It is furthermore held loosely by two cross-bars, $t_1$ and $t_2$, dropped into sockets on the outer wall, a pair of wooden wedges, *w*, being used either to press the panel more firmly against the metal wall or to wedge it farther away from it, as desired. (See Figs. 8, 11, and 13.)

Both panels have provision for adjusting their closure against the corresponding jambs, thus allowing air to leak around their edges at will. Provision must then be made for delivering large amounts of uncontaminated outdoor

[a] Several years' experience has shown that the corners of both panels should be protected by triangular pieces of galvanized sheet-iron to prevent undue wear.

air into the space between these two panels. For this purpose a 4-inch circle is cut in the center of the outer panel $p$ over which is fitted a circular plate with a collar $u$. (See Fig. 13.) An elbow, slightly tapering at one end, connected with the discharge-pipe $q$, is slipped into this collar and thus directs the outdoor air coming from a blower through the pipe $q$ into the open air-space between the two panels of the door, $o$ and $p$. To secure a close fit and thus prevent any inspiration effect tending to suck barn air into the space between the panels, the plate and collar are securely screwed to the outer panel $p$, and the slip joint made by the elbow and collar reenforced by a stout rubber band $v$, cut from a piece of automobile tubing. Under these circumstances, and since the blower delivering air from outdoors is of relatively large size, a strong blast of pure air can be delivered to this air-space. By adjusting

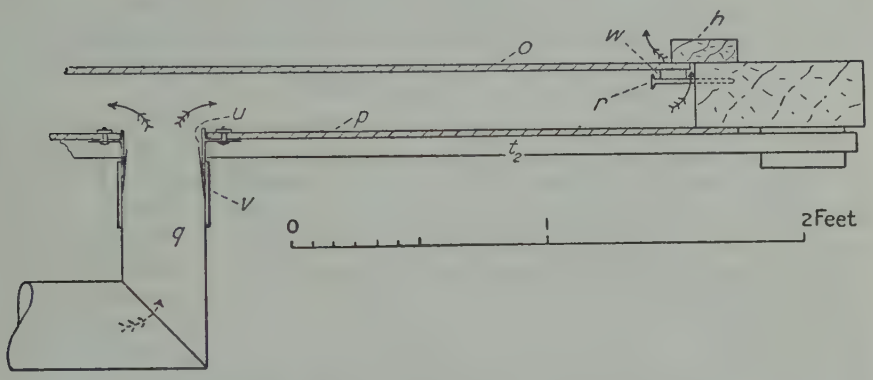


FIG. 13.—Details of closure of double doors on respiration chamber.

Inner door panel $o$, resting against door jamb $h$, is held in place by nails $r$, which set loosely in holes in upright sides of door-frame, and wooden wedges $w$. Outer door panel $p$ is placed over opening of outside sheet-metal wall, allowing a 3-inch air-space between the two panels. Two cross-bars, only one of which, $t_2$, is shown in figure, are dropped in sockets on outer wall to hold panel $p$ in place. Into a 4-inch opening in panel $p$, provided with circular plate and collar $u$, is fitted the elbow from discharge pipe $q$, slightly tapered at the end and held in place by rubber band $v$. Outdoor air directed by blower through pipe $q$ into space between two panels and allowed to leak into respiration chamber around the cracks of inner door panel $o$, as indicated by arrows in the drawing.

the closure of the two panels against their respective jambs (an adjustment simply made by the wooden wedges), just as much pure air may be allowed to leak into the chamber through the imperfect closure of the inner panel as desired, the excess air blowing out around the outer panel, where it loosely touches the metal wall of the chamber. The amount of air thus leaking in around the inner panel is determined, as a matter of fact, by the amount of air discharged from the chamber by the internal blower $B$. If the cracks between the edges of the inner panel $o$ and the door jamb $h$, are too large, especially at the top, actual leakage of air *out* of the chamber may take place. Since the actual amount of air required for ventilating purposes is relatively small, a close fit of the inner door panel is usually desirable, for the larger blower $A$, delivering outdoor air, may be relied upon to furnish pressure enough to *force* sufficient air into the chamber through the cracks around the edge of the door. Under these conditions, therefore, we have secured an out-

door atmosphere on the outside of the *inner* panel of the door of the chamber and the air leaking into the chamber is thus invariably pure outdoor air.

It is of interest to note that these two panels, constructed of commercial compo-board, are so light and transportable that a young girl can easily make this closure and adjustment of the panels in a few moments. This whole procedure, which enables us actually to close the doors, adjust the wedges, and be ready for an experiment in less than five minutes (thus obviating the necessity of closure of the door with rubber gaskets and compression screws, with putty, wax, or any other sealing material), has proved one of the most satisfactory features of the entire apparatus.

To prevent the animal from backing or coming in contact with the thin inner panel of the door, three or four heavy bars of wood, 2 by 4 inches cross-section, are placed on the inside of the upright framework of the door. These either rest directly upon the planks spiked on the inside of the framework, lengthwise of the chamber, or may be dropped into strap-iron sockets.

### Rotary Blower Delivering Outdoor Air.

No method of air delivery compares in efficiency and regularity of motion with the discharge from a rotary air impeller or blower. For our purpose we have used a so-called "Sirocco" blower No. O (manufactured by the American Blower Company), directly connected with an electric motor. This is placed in a small box outside of the barn door, protected from the direct action of rain and snow, and discharges its air through the door into the pipe *q*. For convenience in adjusting the speed of the blower, an external resistance is placed in series with it. Owing to the extreme cold experienced on some days, the ordinary lubricating grease was found to be not so satisfactory as a lighter oil. Without change other than this, the blower has functioned with perfect regularity throughout the five years of its use.

### Air Leaving Chamber.

While the air entering the respiration chamber is of constant composition, i. e., that of outdoor air, there is a varying amount of carbon dioxide added to it by the animal in the chamber. With ruminants, carbon dioxide is derived from two distinct sources: first, and in largest part, that from the lungs, and second, a not inconsiderable proportion derived from fermentations in the intestinal tract, along with varying amounts of methane. Our main problem is the measurement of the total amount of carbon dioxide produced by the animal, irrespective of its source. Inside the respiration chamber there is a considerable difference in the composition of the air, since that nearest the door would have the lowest percentage of carbon dioxide and that nearest the animal's nostrils would have the highest. To secure as even a distribution of carbon dioxide as possible throughout the whole air, an electric fan is placed in the chamber at the rear end, blowing air diagonally across the top. This is an essential feature of the apparatus. The discharge of the air from the chamber may be made at almost any point, provided it is not too near the door. Theoretically at least, it should be discharged from the front end of the chamber, that is, farthest from the point where the fresh air enters. As a matter of fact, for the sake of convenience in the particular construc-

tion employed at Durham, we found it advantageous to remove it at a point about half way along the side, near the bottom of the chamber. By means of the electric fan, however, the air in the chamber is so thoroughly stirred as to make the actual point of withdrawal of little significance.

The discharge of air from the respiration chamber should be made at such a rate as to hold the carbon-dioxide percentage approximately 1.0 or below. It is unnecessary to note the exact volume of air discharged, and hence no meter-pump or large gas-meter for the entire ventilating current is necessary. For the largest sized steer we have found sufficient a small "Sirocco" blower, No. 00, which has a $\frac{1}{70}$ h. p. motor directly attached to it. For minor adjustments of air withdrawal, an external resistance in series with this blower, controllable from outside the chamber, is very helpful. The discharge opening is about 2 inches in diameter, and this is connected directly with a small 2-inch length of sheet-copper tube which should extend through the metal wall of the chamber on the inside for an inch or two and on the outside an equal distance. The discharge of the blower is brought directly in contact with this 2-inch pipe, and the closure well made with a stout rubber band. Obviously the blower should be protected from any contact with the animal's hoofs, and we have found it desirable to cover the whole blower with a piece of fine-meshed wire netting to keep out dust and hair that might interfere with the functioning of the blower. The other end of the 2-inch pipe through the wall is connected by means of a piece of rubber tubing (as a matter of fact, we have used a short section of automobile tubing) with a 2-inch thin-walled pipe attached to the air-sampling chamber or wind-chest. A light spiral spring placed inside of the 2-inch rubber tubing prevents its collapsing, although it is important to note that there is but a slight positive pressure on this tubing. By placing the blower inside of the respiration chamber all danger of leaks around the blower is avoided. Furthermore, it is very accessible and can be easily removed or cleaned. Obviously, in any duplication of the apparatus, the location of the discharge blower should take into consideration the relative location of the respiration chamber and the accompanying small laboratory beside it, in which the sampling apparatus and carbon-dioxide absorbing vessels are placed.

### Principles Underlying Aliquoting and Analysis of Ventilating Air Current.

The only constituent of the air that is determined is carbon dioxide, and since it is impracticable to absorb the entire amount of carbon dioxide from so large a current of air as is necessary to ventilate the chamber, a method of sampling or aliquoting the outgoing air is essential. Directing a current of air into a closed box with two circular orifices will result in the escape through these openings of volumes of air approximately proportional to their areas. In this apparatus air is discharged from the respiration chamber into a metallic wind-chest (*A*, Fig. 14) with two openings, one (*E*) about 10 mm. in diameter, fixed in size and conducting air into the bottom of a can *F* with a rubber bathing-cap top. The other opening (*D*) leads directly to the air, and its diameter may be varied at will from a maximum of 97 mm. to as small as desired, by means of caps with various-sized circular openings in them. In the cap, which is immersed in water in a water-seal (see *D*, Fig. 14), a hole of

suitable size is drilled. For all of our work with steers, the diameter of this opening in the cap was 29 mm. Since the amount of air escaping through the two openings will be approximately proportional to the areas of the openings, it can be seen that about 10 per cent escapes through the 10-mm. opening *E*, and 90 per cent through the 29-mm. opening *D*. Subsequent tests have shown this relationship to be very close. As a matter of fact, with this combination of 29-mm. and 10-mm. openings, respectively, 10.20 per cent is the proportion escaping through the smaller opening. To have this proportion remain constant, it is necessary that the air be discharged in both instances with a free discharge. From an examination of the diagrams (Figs. 6 and 14), it can be seen that in one instance the air is discharged into the room free, namely, through the larger opening, while in the other case it is discharged into a can with bathing-cap cover, light to be sure, and flexible, but nevertheless a cover. Since it is a prerequisite for the method of sampling that there must be free discharge from both openings, some device is essential to insure that the air passing through the small 10-mm. opening *E* will, as a matter of fact, be discharged always against atmospheric pressure and not be hampered by the pressure of the bathing-cap. Of still greater importance is the fact that the air leaving this small opening and entering the sampling-can is actually to be used as a sample, and hence if both conditions are to be maintained (free discharge against atmospheric pressure and control of the sample after being discharged), it is necessary that provision be made for withdrawing the air from the sampling-can just as fast as it is discharged into it. The air withdrawn from the sampling-can is forced through suitable absorbers to retain the carbon dioxide.

The exact size of the opening into the sampling-can, the amount of air delivered into it per minute, and particularly the adjustment of the proportionality between the sample and the total air current depends upon several factors; among these the total carbon-dioxide production of the animal, second, the length of the period, and third, the limit of error in weighing the absorbing vessels. Taking into consideration all of these factors, practice has demonstrated that the 10-mm. opening and the rotary air-impeller used to discharge air from the respiration chamber into the sampling-can will permit approximately from 30 to 40 liters of air per minute to enter the sampling-can, and since this is approximately 10 per cent of the total and the other 90 per cent escapes into the air, it can be seen that the total ventilation of the respiration chamber by this device is not far from 300 to 400 liters of air per minute, an intensity of ventilation amply sufficient to hold down the carbon-dioxide percentage of air inside the chamber to 0.5 or below, even with a full-grown steer.

The efficiency of the rotary air-impeller, blower *B* (see Fig. 6), discharging air from the chamber determines in large part the actual delivery of air into the sampling-can *F* (see Fig. 14), and the efficiency of the blower in turn depends upon the voltage. With reasonably uniform voltage a total ventilation of 300 to 400 liters per minute is assured. Under these conditions there is a slight positive pressure inside the wind-chest, which, as a matter of fact, amounts to not far from 8 to 11 mm. of water with the size of orifices (10 and 29 mm.) we employed.

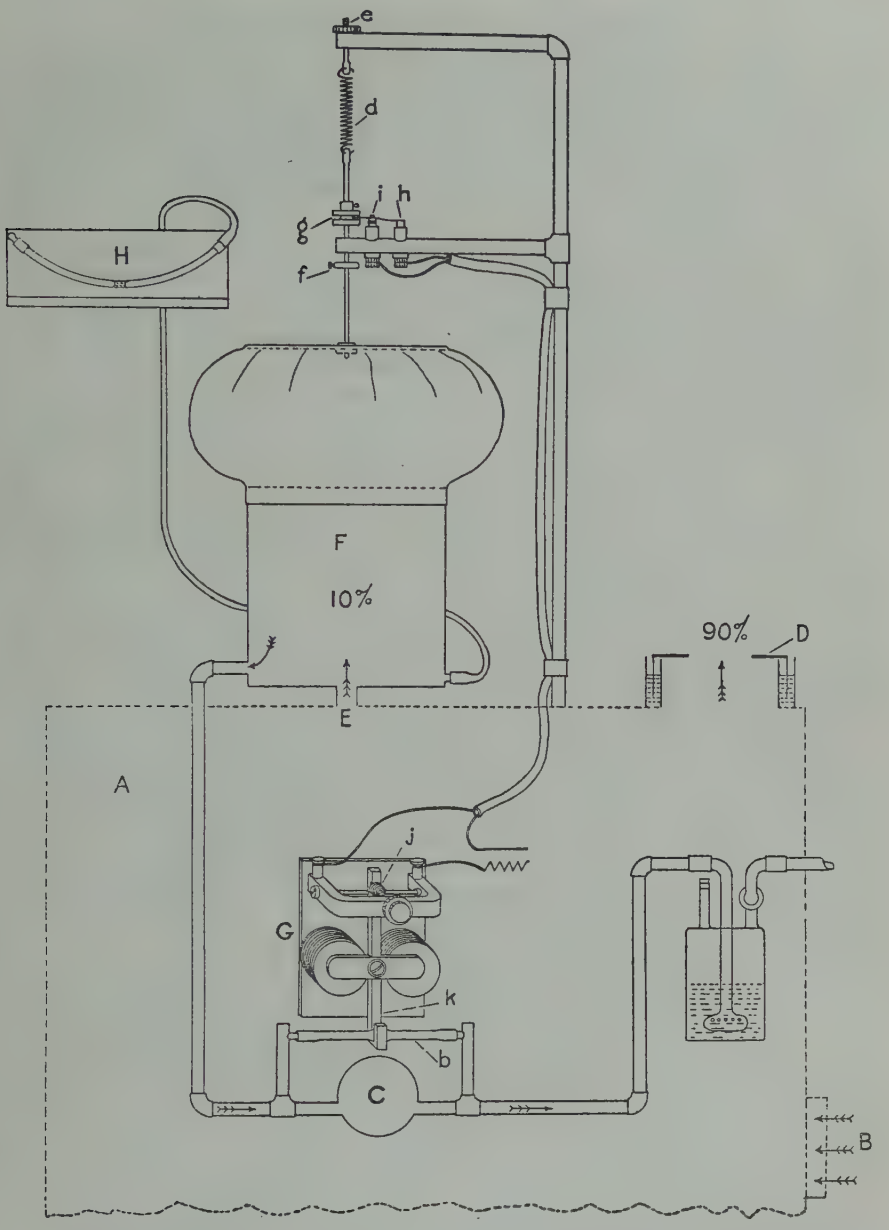


FIG. 14.—Details of device for insuring atmospheric pressure inside sampling can.

*A*, wind-chest; *B*, opening for entrance of air from respiration chamber. *D*, cap immersed in water-seal with opening for delivery of major portion of air to outside; cap consists of a brass disk approximately 105 mm. in diameter and 1.5 mm. in thickness, with a hole 29 mm. in diameter cut in its center; the disk is soldered into the end of a tube formed up of a band of brass or copper 43 mm. in depth and 1 mm. in thickness. *E* opening for delivery of sample of air into can *F*. The weight of the bathing-cap on top of can *F* is counterpoised by spring *d*, the tension of which is regulated by nut *e*. The brass rod connecting spring *d* with rubber bathing-cap extends inside bathing-cap, and to its lower end is attached a light aluminum plate held in place by nuts above and below. Fiber stop *f* prevents spring *d* from rising too far. A thin, flat spring *h*, the tongue of which rests in a groove in a fiber spool, *g*, actuates two tungsten contacts at *i*, through which an electric current is passed to the telegraph sounder *G*. A spring, *j*, controls pressure of armature lever *k*, which automatically opens and closes by-pass *b*, thus deflecting a portion of air from main air current and thus regulating withdrawal of air from can *F*, so that petroleum manometer *H* always indicates atmospheric pressure inside can *F*.

### Removal of Air from Sampling-can.

To prevent back pressure in the sampling-can, which would be disastrous to the proper discharge of air through the 10-mm. opening, and to dispose of the air sample, air must be withdrawn from this sampling-can as rapidly as delivered, and thus conditions of equilibrium secured in the can. While both the blower *A*, delivering air into the respiration chamber, and blower B, delivering air from the respiration chamber to the wind-chest, are of the rotary air-impeller type, the blower *C* (see Figs. 6 and 14) withdrawing air from the sampling-can must be of the positive type, so as to force the air through sulphuric acid for the removal of water-vapor, and through soda-lime for the removal of carbon dioxide. The sampling can *F* (see Fig. 14) is covered with a bathing-cap, carefully counterpoised and suspended by a light spiral spring, *d*. If the air is withdrawn from the can at such a rate as to maintain exact atmospheric pressure within the can, this is the equivalent of having air discharged from the wind-chest through both openings into a free atmosphere. The withdrawal of air from the sampling-can and its passage through sulphuric acid and soda-lime permit a quantitative absorption of carbon dioxide in vessels which can be accurately weighed and thus the weight of carbon dioxide in the aliquot passing through the sampling-can is accurately determined in periods of any desired length.

Theoretically, one might consider it possible to connect to one electric motor and possibly on the same armature shaft two blowers, so that the exact discharge into the sampling-can and the withdrawal at the same rate would be accomplished without further adjustment, i. e., both blowers having the same shaft speed. This is impracticable, since one blower discharges against free atmospheric air and has a free air intake. The other blower (positive) must discharge air through absorbing vessels, the resistance of which changes every time the air is deflected from one set of purifiers to another. The most delicate adjustment, however, of this balance between discharge into the sampling-can and withdrawal from it can be made by an automatic regulation of the suction of the positive blower. In the earliest form of this type of apparatus[a] and, indeed, during the first year's work at Durham, a Crowell blower (so frequently used in the Nutrition Laboratory on universal respiration apparatus), belted to an electric motor, was employed. Subsequently a much more positive and less troublesome combination has been obtained by using a smaller (less effective) blower, the so-called "Cenco" blower, and, indeed, directly connected to the armature shaft of a $\frac{1}{8}$ h. p. electric motor with a speed of not far from 1,700 revolutions per minute. Under normal conditions of running, the suction is relatively proportional to the shaft speed. The details of the blower, by-passes, and accessory piping are shown in Fig. 15.

The rotor of the blower has three fiber blades, weighted on the inside with lead (shown in heavy black line in the figure). These are pressed by centrifugal force at the high speed of revolution against an eccentric air-chamber. At the speed at which the blower ordinarily runs, about 35 liters of air per minute are taken in on the suction side, that is, somewhat more than the amount ordinarily discharged into the bathing-cap can by the rotary blower *B*, through the opening in the wind-chest. Since the positive blower draws

[a] Benedict, Miles, Roth, and Smith, Carnegie Inst. Wash. Pub. No. 280, 1919, pp. 103 et seq.

a little more air than is ordinarily delivered, it is necessary to lower the effective suction of the blower by means of by-passes. These consist of connections between the suction and positive side of the blower, one through the ⅛-inch standard-sized pipe *a*, controlled by a petcock *c*, and the other through a small, thin-walled, rubber tubing *b*. When petcock *c* is wide open obviously there is little effective suction, since the air simply goes in a circle

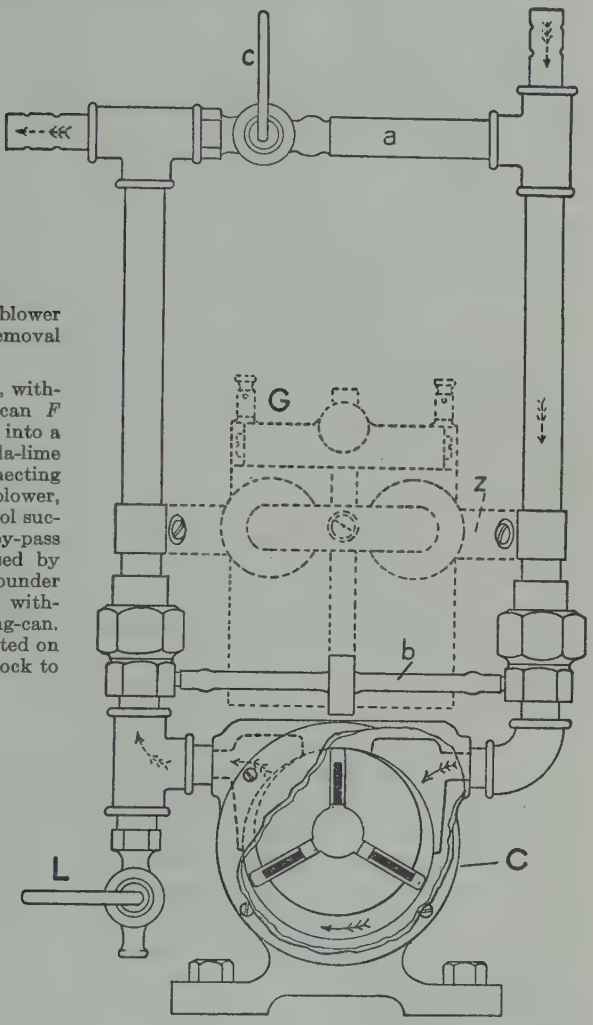


FIG. 15.—Details of positive blower and by-passes controlling removal of air from sampling-can.

A positive, 3-blade blower, *C*, withdraws air from the sampling-can *F* (Fig. 14), and causes it to flow into a chain of sulphuric-acid and soda-lime bottles. Main by-pass *a*, connecting suction with pressure side of blower, is fitted with petcock *c*, to control suction. A second rubber-tube by-pass *b*, electrically opened and closed by automatic action of telegraph sounder *G*, insures closer regulation of withdrawal of air from sampling-can. Telegraph sounder *G* is supported on pipes by brass yoke *z*. *L*, petcock to drain extra oil from blower *C*.

from the high-pressure side back to the low-pressure. On the contrary, when the petcock is fully closed, the maximum effect of the blower is secured. In practice this by-pass is always nearly completely closed. It does serve, however, to help in gross adjustments. But for the final and more delicate adjustments, the supplementary by-pass *b* is necessary. To control the air flowing through *b* an extension of the armature of an inexpensive telegraph sounder *G* (Fig. 14) is so adjusted as to compress the thin-walled tubing *b*

by the normal tension of the telegraph-sounder spring. When the current is passed through the field coils, the armature is drawn down and consequently the pressure against the tube *b* released and air can rush through it at full capacity, and in so doing obviously has the effect of curtailing the effectiveness of the suction of the blower. To actuate this apparatus the electric current is connected in such a manner that the slightest alteration in the level of the bathing-cap will open or close metallic contacts in the circuit. The magnet has a resistance of about 5 ohms and may be connected with a battery, or in case direct current is used, with a suitable drop-wire or series resistance.

The counterpoising spring sustaining the weight of the bathing-cap (see *d*, Fig. 14) is attached to a small rod upon which is attached a small fiber spool *g*. In a narrow groove on the spool rests the tongue of a thin, flat spring *h*, 28 mm. long. If the bathing-cap rises a fraction of a millimeter, this flat spring is likewise raised and the contacts at *i* are broken. These contacts are of tungsten to prevent pitting. The fact that the bathing-cap has risen shows that sufficient air is not being withdrawn from the sampling-can; in other words, that the positive blower *C* is somewhat ineffective. This in turn shows that too much air is passing through the by-pass *b*. When the electric contact is broken by the separation of the tungsten points, the telegraph-sounder magnet ceases to act and the stout spring *j* of the sounder presses the extension of the armature shaft against *b*, so as to close it. As a result of this, the blower instantly becomes in turn a trifle too effective, the bathing-cap starts to sink, the electric contact at *i* is now made, and the armature is drawn by the magnet so that the armature extension *k* diminishes its pressure against the rubber tubing, thus opening by-pass *b*, allowing air to flow through it, and thus, in turn, diminishing the effectiveness of the blower.

While, therefore, the rate of revolution of the blower shaft remains practically constant, fluctuating only with the voltage, the delicate adjustment of the actual withdrawal of air from the sampling-can is made by means of this electro-magnet by-pass, the making and breaking of the circuit being repeated continuously at intervals of fractions of a second, thus resulting in the most delicate regulation of air-flow through the absorbing system. It was soon found that the adjustment could be made so perfect as to insure uniform atmospheric pressure inside the rubber bathing-cap, the criterion being a delicate petroleum manometer *H*, attached to the sampling-can *F*. (See Fig. 14.) This mechanism, therefore, meets the demands of the aliquoting system, namely, to make it possible to discharge air from the wind-chest through one opening against atmospheric pressure and through another opening into a sampling-can, likewise continually maintained at atmospheric pressure. The mechanism, furthermore, makes it possible to collect the air sample completely and pass it through suitable absorbents for retaining quantitatively the carbon dioxide.[a] Although we have not used it for this purpose, it is obvious that

[a] In all of the work at the Nutrition Laboratory direct current is available, and consequently all the blowers, both rotary and positive, are connected with direct-current 110-volt motors. This current, by means of suitable resistances, was likewise used to actuate the electrical by-pass. In installing the apparatus at Durham, we found that the usual electric service was an alternating current, although a rotary transformer giving 110 volts direct current was available. This has been the source of considerable annoyance, owing to breakdowns in the power line, the use of apparatus for experimental work in the college, and for other reasons. In any new construction it is not impossible that the entire electrical system would best be furnished with alternating-current motors, and in this case either a storage battery or dry batteries will be necessary to actuate the electrical by-pass.

the aliquot may subsequently be used to determine methane, if desired. A somewhat diagrammatic arrangement of the sampling-can, wind-chest, and particularly the electric by-pass, is given in Fig. 14.

The adjustment of the two by-passes to the blower is very simple, as standard ⅛-inch piping is used and no mechanical difficulties are present. The telegraph sounder, which draws about 0.65 ampere, is an inexpensive form sold under the trade name of "Mesco."

The Durham apparatus uses only one sampling-can and blower, but with the group respiration chamber at the Nutrition Laboratory two sampling-cans,[a] attached to a wind-chest in common, each with its positive blower and double set of purifiers, have been installed. Where experiments with animals can be made in short, easily repeated periods, duplicate samples are hardly necessary. With the costly, time-consuming 24-hour experiments, in all probability the double installation is desirable. The agreement between the two sets of carbon-dioxide absorbing vessels, where the two sampling-cans are used, is almost invariably perfect. Experience covering 3 years' work with the double apparatus at the Nutrition Laboratory has shown that of a total of 158 experimental periods there were no instances after the first year's work where the duplicates did not agree within 2 per cent and usually very much closer. Where the duplicate installation is desired, instead of using the two Crowell blowers outlined in the original description of the Nutrition Laboratory apparatus, we have recently attached two Cenco blowers to the same armature shaft of a ⅙ h. p. electric motor, each blower having its independent set of by-passes and electric connections with the respective sampling-cans. This apparatus has functioned perfectly for somewhat over a year and is strongly to be recommended.[b] It should be emphasized that the Cenco blower is not absolutely air-tight, since minor leaks around the shaft may be expected. It may not, therefore, be used for any closed-circuit apparatus, and hence cannot take the place of the Crowell blower for this latter purpose, but it is admirably adapted for the present apparatus, where slight leaks are of absolutely no significance.

### Absorption Apparatus.

Having provided for the adjustment of the withdrawal of air from the sampling-can to equal the amount of air delivered to it, it is necessary to absorb quantitatively the carbon dioxide from the air sample and, indeed, in suitable vessels that can be weighed. The air leaving the respiration chamber contains carbon dioxide and water-vapor, and after leaving the blower is first passed through bottles containing sulphuric acid to remove the water-vapor, next to bottles containing soda-lime to remove carbon dioxide, and finally to a bottle containing sulphuric acid to collect the water given off by the soda-lime. We have found nothing equal to the Williams bottle for the absorption of water-vapor by sulphuric acid, in an air current amounting to 30 liters or more per minute.[c] One Williams bottle, freshly charged with 450 c. c. of

[a] Benedict, Miles, Roth, and Smith, Carnegie Inst. Wash. Pub. No. 280, 1919, pp. 103 et seq.

[b] The single-blower apparatus is the Cenco blower, No. 1400-C, furnished by the Central Scientific Company, Chicago, Illinois.

[c] The details of the special form of bottle used for holding the soda-lime, and particularly of the Williams bottle for sulphuric acid, can be found by referring to Carpenter, Carnegie Inst. Wash. Pub. No. 216, 1915, pp. 27 and 28. The glass parts of the Williams bottle are obtained from E. Machlett & Son, 153 East Eighty-fourth Street, New York City.

sulphuric acid, will absorb 10 grams of water-vapor without allowing a weighable amount to pass in a current of air of 35 liters per minute. After this limit has been exceeded, it is necessary to have a second Williams bottle in the series. Common practice has shown that it is best to have two Williams bottles after the blower. The first may therefore be allowed to gain an indefinite amount of water, provided the second does not exceed the limit of 10 grams. The air then enters the soda-lime bottles and finally a Williams bottle, which again must not be permitted to gain over 10 grams. When this last Williams bottle has reached its weight limit, it is usually placed next the blower, and thus the sulphuric acid may be more completely exhausted before being rejected.

The soda-lime may be held in any wide-mouthed bottle with good-fitting rubber stopper and two pipes of sufficient diameter. A form which has been developed at the Nutrition Laboratory and has given excellent service makes use of the standard 1-gallon fruit jars (see diagram in Fig. 16). An extra long wire clip or bail is provided and two fruit-jar rings used to make the closure. Between the glass cover and the mouth of the bottle is placed a heavy metal piece of tubing, through which two pipes are soldered, one leading to the bottom of the jar and the other extending just through the brass ring. To these pipes are attached the usual short pieces of pure-gum rubber tubing and standard ¾-inch hose couplings. This closure is most satisfactory and very rapidly made. The cover may be removed and pipes withdrawn for cleaning in an instant. The direction of the air-flow is such as to have the air enter at the top of the jar and leave through the pipe at the bottom. Under these conditions the soda-lime on the top of the bottle becomes exhausted first, as noted by the whitening of the product, and can be easily scraped out and a fresh supply inserted, even if the bottle itself is not completely exhausted.

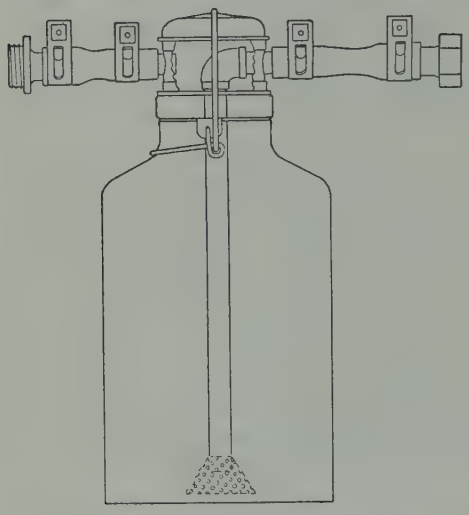

FIG. 16.—Details of soda-lime bottle used in absorption system.

The sulphuric-acid Williams bottle must follow the soda-lime bottles to collect the water-vapor normally given off by the slightly moist soda-lime to the dry air current. By weighing the soda-lime bottles and the following sulphuric-acid bottle, the increase in weight of this combination may be taken as representing exactly the weight of carbon dioxide in the air passing through them. The discharge of the air from the last sulphuric-acid bottle carries with it an unweighable but nevertheless distinctly acid fume, which in a small closed laboratory might become unpleasant to the operators. We have therefore usually diverted this final discharge of air through a metal

container or can (see S, Fig. 6), filled with loose cotton batting, into which dry sodium-bicarbonate has been loosely sifted. The air issuing from this can is always perfectly respirable.

The carbon dioxide absorbed in the soda-lime bottles consists for the greater part of that produced by the animal, but there is a definite amount normally present in the pure outdoor air entering the chamber. This should be determined and must be deducted from the total weight to make proper correction. To compute this carbon dioxide it is only necessary to know approximately the volume of air in the sample, and to determine this the air is finally passed through an ordinary 3-light commercial dry gas-meter, preferably one constructed for the foreign trade and hence graduated in liters.

The air sample can be passed through one set of purifiers and the carbon dioxide quantitatively absorbed until the amount of water-vapor collected in the last Williams bottle approaches 10 grams, when a new set of purifiers must be employed. In practice it is desirable to change the set of purifiers every half hour, and thus obtain a series of accurately determined carbon-dioxide measurements in short periods. To do this it is necessary to deflect the air current from one set of purifiers to another. This is done by means of a 3-way valve[a] ($V_1$, Fig. 6). The second set of purifiers differs in no wise from the first. While we have ordinarily used a 3-way valve, $V_2$, to direct the air *issuing* from the second set likewise through the meter, danger has occasionally been experienced in that operators have turned the two valves in opposite directions and thus caused a building-up of pressure and a back discharge of sulphuric acid, which either comes in contact with the soda-lime, usually resulting in an almost explosive destruction of the bottle, or which backs up into the blower, necessitating immediately taking down the blower and thoroughly rinsing with water and freeing from acid. We recommend, therefore, that the second 3-way valve be not used and that the metering of the alternate samples be dispensed with, or that two meters be connected, one for each set of purifiers.

### Determination of Carbon Dioxide.

The apparatus, as described above, ventilates the chamber, secures a sample of air, and forces it through proper absorbing vessels. Since the two openings in the wind-chest have the relationship of 10 to 90, approximately 10 per cent of the carbon dioxide is thus collected and weighed, but, as already pointed out, in this amount of carbon dioxide there is a small amount due to the carbon dioxide normally present in the air entering the respiration chamber, and consequently a correction is necessary. The correction is relatively small, and hence excessive refinement in its determination is not necessary. Repeated analyses of uncontaminated outdoor air[b] show that the carbon-dioxide content is constant, 0.03 per cent by volume, irrespective of weather conditions, temperature, or season. As can be seen from the construction of the door and the method of allowing air to enter the chamber, it is impossible to measure the volume of outdoor air introduced into the chamber, but for every liter of air leaving the chamber a liter of air must leak in around the door, and this air carries with it a definite amount of carbon dioxide. To

[a] 3-way valve with two ports in the plug.
[b] Benedict, Carnegie Inst. Wash. Pub. No. 166, 1912, p. 114.

determine this, blank tests are made in which only pure outdoor air is passed through the entire aliquoting and carbon-dioxide absorbing system, and by noting the reading on the gas-meter and the increase in weight of the carbon-dioxide bottles, it is possible to establish definitely the correction for the outdoor air. This obviously depends in part upon the accuracy of the meter and, theoretically at least, upon the temperature of the air and the barometric pressure. For practical purposes, at sea-level in Boston, it has been found that by running the air through a set of purifiers for from 4 to 6 hours a constant can be readily secured. This corresponds to not far from 0.59 gram carbon dioxide per 1,000 liters.[a] By reading, therefore, the difference in the meter between the beginning and end of the period and applying this correction of 0.59 gram per 1,000 liters to the reading, a proper deduction from the total weight of the carbon dioxide due to that entering with the outdoor air may be made.

Of the greatest importance, though, is the establishment of the relationship between the true amount of carbon dioxide thus collected in the sample and the total amount leaving the chamber through both orifices. Theoretically at least, these amounts should be closely proportional to the areas of the openings leading from the wind-chest, i. e., approximately 10 and 90 per cent, respectively. Instead of relying upon calculation, it seemed best, in view of the possibility of the development of eddy currents, peripheral frictional variations due to the differences in size of holes, etc., to make a chemical calibration of the apparatus to establish this relationship. Prior to the closing of the chamber doors a rubber tube is connected with a small pipe in the wall and the end placed well into the intake of blower *B*. On the outside of the respiration chamber connection may be made with the source of carbon dioxide. The chamber doors are then closed and the chamber thoroughly ventilated until it is filled with uncontaminated outdoor air. A definite amount of pure carbon dioxide is then conducted through the tube into the intake of blower *B*. By this means all the carbon dioxide is delivered into the wind-chest and none can get back into the respiration chamber.

### DETAILS OF TESTS OF THE APPARATUS.

Usually these calibration tests of the aliquoting device are of short duration, 20 minutes or less, during which time 50, 60, or more grams of carbon dioxide may be introduced, of which approximately one-tenth is weighed in this sample, i. e., 5 grams, and the correction for outdoor air in this time would be but about 0.3 gram. As a source of carbon dioxide we have used very successfully the small steel bottles holding about 5 pounds furnished by the liquid carbonic-acid concerns. These may be weighed on the balance used for weighing the absorbing vessels, and 50 or more grams may be introduced with an error in weight considerably less than 0.1 gram. Under these conditions the percentage collected in the sample can be determined with great exactness, and repeated tests not only of the proportion of air discharged through the 10-mm. and 29-mm. openings but likewise through openings of various other sizes have shown that this relationship may be easily established well within 1 per cent. As a matter of fact, in the Durham apparatus

[a] In certain of our tests a meter graduated in cubic feet was used and the factor 1.6 grams carbon dioxide per 100 cubic feet of outdoor air was employed.

the exact proportion passing through the 10-mm. opening has been found to be 10.20 per cent.

Thus far no balance has been found that compares for the express purpose of weighing either the carbon-dioxide cylinders or more particularly the soda-lime and Williams bottles with that manufactured by August Sauter in Ebingen, Württemberg, Germany. The absorbing bottles can be weighed to within 1 centigram. Consequently we have found it advantageous to collect not less than 5 or 6 grams of carbon dioxide in each period, and either the length of the period or the proportion of air discharged into the sampling-can may be altered arbitrarily so that the amount of carbon dioxide collected in the absorbing system will be 5 grams or above for each period.

### Correction for Residual Carbon Dioxide.

Having established the relationship between the volume of the sample and the total volume withdrawn from the chamber, the determination of the carbon dioxide withdrawn from the chamber is relatively simple, but before the true measure of the carbon dioxide produced by the animal inside the chamber can be found, any changes in the residual carbon-dioxide content of the air in the chamber must be accurately known and corrections therefor made. Obviously, the smaller the extraneous volume of air about the animal the more rapidly will the air be changed in the chamber. For long experiments the residual carbon dioxide may practically be disregarded. For short experiments it is important to take it into consideration, particularly during the first half hour after the animal has been placed inside the chamber and before the equilibrium between carbon-dioxide production and ventilation-rate of the chamber has been perfectly established. The carbon-dioxide content of the air in the chamber must be directly determined. In our regular work we have found most useful the Haldane apparatus for carbon dioxide only,[a] which permits the measurement of carbon dioxide to 0.001 per cent very rapidly. It will be recalled that the carbon dioxide in the chamber is purposely held at between 0.25 per cent and 0.50 per cent. At the beginning and end of each period a sample is taken and analyzed. With the Haldane apparatus care is necessary to keep it very clean, particularly the mercury, and in cold weather one should be sure that the water-bath is not allowed to freeze.

The sample may be taken in a number of ways, either, as is the case in the Boston apparatus, by having the gas-analysis apparatus directly connected with a small pipe through the wall of the chamber, or as in Durham, by connecting the gas-analysis apparatus with a pipe coming from the high-pressure side of the positive blower. Either position gives satisfactory results. Having determined the carbon dioxide in the air, the computation of the residual amount involves a knowledge of the total air volume inside the chamber, which obviously is readily obtained by simple computation from the cubical contents, making allowance for the volume of the animal and that of the wooden framework. Although, theoretically, at the time of each computation the volume of the air should be reduced to 0° C. and 760 mm., for all practical purposes it has been found that a simple factor may be readily computed and that each difference of 0.001 per cent carbon dioxide may be expressed in terms of a

[a] See Haldane, Methods of air analysis, London, 1918, 2d ed., p. 68.

definite weight in grams of carbon dioxide. With the Durham apparatus (air volume circa 9,000 liters) this correction amounts to 0.18 gram carbon dioxide for each 0.001 per cent of this gas found in the air.[a]

TABLE 6.—*Typical calculation of a period during a carbon-dioxide check test.*

(9h26m to 9h51m a. m., June 13, 1919.)

| | | |
|---|---|---|
| Weight of absorbing vessels at end | gm. | 9,348.22 |
| Weight of absorbing vessels at start | gm. | 9,342.77 |
| $CO_2$ absorbed from aliquot of outgoing air | gm. | 5.45 |
| Volume of aliquot of outgoing air | cu. ft. | 35.4 |
| $CO_2$ in aliquot from outdoor air[1] (0.354×1.6) | gm. | 0.57 |
| $CO_2$ in aliquot from chamber (5.45−0.57) | gm. | 4.88 |
| $CO_2$ in total outgoing air[2] $\left(\frac{4.88}{10.20}\times 100\right)$ | gm. | 47.84 |
| Residual $CO_2$ in chamber at end | p.ct. | 0.333 |
| Residual $CO_2$ in chamber at start | p.ct. | .290 |
| Change in residual $CO_2$ | p.ct. | .043 |
| Change in residual $CO_2$ corrected[3] (0.18×0.043×1,000) | gm. | 7.74 |
| $CO_2$ corrected by residual (47.84+7.74) | gm. | 55.58 |
| Weight of steel cylinder at start | gm. | 4,485.6 |
| Weight of steel cylinder at end | gm. | 4,429.4 |
| $CO_2$ admitted to chamber | gm. | 56.2 |
| Per cent $CO_2$ withdrawn from chamber $\left(\frac{55.58}{56.20}\times 100\right)$ | p.ct. | 99 |

[1] Estimated that each 100 cubic feet of outdoor air contains 1.6 grams carbon dioxide.

[2] 10.20 equals percentage of total outgoing air actually passing through absorption system, i. e., when the 29-mm. opening is used. A simpler calculation would be to multiply directly by the factor $9.80\left(\frac{100}{10.20}\right)$.

[3] Estimated that each 0.001 per cent carbon dioxide corresponds to 0.18 gram carbon dioxide, as the volume of air in the chamber is about 9,000 liters.

### COMPLETE TEST OF RESPIRATION APPARATUS.

A complete test of the accuracy of the apparatus in determining carbon dioxide can be made much on the same basis as the calibration of the proportion that the sample bears to the total air current, namely, by admitting known weights of carbon dioxide from a steel bottle into the chamber, in this case, however, not introducing it directly into the blower but having the discharge pipe at approximately the position of the nostrils of the animal. The electric fan continually stirs the air in the chamber, the residual analyses are made as usual, and corrections applied in the final calculations. A typical example of a single experimental period is given in Table 6 and a summary of the results of an entire experiment in Table 7.

[a] At this point an error in the original description of the Durham apparatus should be brought to attention. (See Benedict, Collins, Hendry, and Johnson, New Hampshire College Agricultural Experiment Station, Technical Bulletin No. 16, April, 1920.) Throughout this entire description, particularly on pages 23, 24, 25, and 26, there is an erroneous statement made that the correction is 1.8 grams for each 0.001 per cent. As a matter of fact, all of the calculations in the tables and reported results are correctly given, but the factor reported is wrong, as it should be 0.18 gram instead of 1.8. (It is of interest to note that the entire bulletin, fortunately with the above correction, has been translated into French and printed in the Bulletin Société Scientifique d'Hygiène Alimentaire, 1921, 9, p. 501.)

The carbon dioxide collected in the absorbers has been found from an extensive series of calibration tests to correspond to 10.20 per cent of the total amount leaving the chamber. In this particular period, illustrated in Table 6, therefore, the total amount of carbon dioxide leaving the chamber, corrected for that entering with the incoming air, was 47.84 grams. There was, meanwhile, an increase in the carbon-dioxide percentage in the air of the chamber, amounting to 0.043 per cent, which corresponds to 7.74 grams. Hence the total carbon dioxide, corrected by this residual, is 55.58 grams actually determined by the apparatus, while from the difference in weight of the steel cylinder at the start and the end it is found that 56.2 grams were admitted. In other words, 99 per cent of the total carbon dioxide admitted was recovered.

TABLE 7.—*Summary of carbon-dioxide measurements during a check test with the respiration chamber, June 13, 1919.*

| Time of end of period. | Residual carbon dioxide in chamber by analysis. | (*a*) Change in residual content of carbon dioxide.[1] | Analysis of aliquot. (*b*) Carbon dioxide from incoming air. | (*c*) Carbon dioxide absorbed from outgoing air. | (*d*) Carbon dioxide corrected for amount from incoming air ($c-b$). | (*e*) Carbon dioxide in total outgoing air[2] $\left(\frac{d}{10.2}\times 100\right)$ | (*f*) Carbon dioxide in total outgoing air corrected by residual ($e \pm a$). | (*g*) Carbon dioxide admitted to chamber. | (*h*) Per cent carbon dioxide withdrawn from chamber $\left(\frac{f}{g}\times 100\right)$ |
|---|---|---|---|---|---|---|---|---|---|
| | *p. ct.* | *gm.* | *gm.* | *gm.* | *gm.* | *gm.* | *gm.* | *gm.* | *p. ct.* |
| 8h36m a. m. | 0.226 | ..... | ..... | ..... | ..... | ..... | ..... | ..... | ..... |
| 9 01 a. m. | .297 | +12.78 | 0.58 | 5.43 | 4.85 | 47.6 | 60.3 | 61.3 | 98 |
| 9 26 a. m. | .290 | − 1.26 | .57 | 5.58 | 5.01 | 49.1 | 47.9 | 47.4 | 101 |
| 9 51 a. m. | .333 | + 7.74 | .57 | 5.45 | 4.88 | 47.8 | 55.6 | 56.2 | 99 |

[1] Estimated that each 0.001 per cent carbon dioxide corresponds to 0.18 gram carbon dioxide.
[2] 10.20 equals percentage of total outgoing air actually passing through absorption system.

Given the equipment for making respiration experiments as a whole (the balance and the cylinder of liquefied carbon dioxide), no procedure more rigidly controls the apparatus than these gas-checks and it is our custom to make them very frequently throughout the winter. If the apparatus can recover a known amount of carbon dioxide admitted to within 1 or 2 per cent, it is reasonable to assume that it can likewise determine the carbon-dioxide production of a steer to within this degree of accuracy. Hence we strongly recommend frequent gas-checks on all important work.

## SPECIAL USES OF THE RESPIRATION CHAMBER.

Although the apparatus was designed primarily for short experiments (that is to say, three or four half-hour periods), and, indeed, for individual large domestic animals, it has likewise been successfully used for 24-hour experiments on a steer. The animal was, however, given feed immediately prior to entering the chamber, was provided with a special bag for feces collection, and wore a urine funnel. The apparatus has likewise been extensively used throughout the entire winter of 1920–21 for studying groups of smaller animals, particularly sheep and calves. Of special interest is the fact that this apparatus can be operated by not more than two assistants, save in the case of 24-hour experiments, where relief is necessary. While the scientific returns

from this newer form of respiration chamber can not properly be compared with the complete and elaborate analysis of metabolic processes made possible by the intricate respiration calorimeter in the Institute of Animal Nutrition at State College, Pennsylvania, nevertheless the relatively small cost of installation of our apparatus and the slight expense of operation should make possible the accumulation of a considerable amount of data on the nutrition of domestic animals, at present prevented by the prohibitive cost of the older and more elaborate apparatus. We have, therefore, in the present apparatus an accurate method of measuring the carbon-dioxide production of domestic animals, either in groups or, as in the case of the present research, individual animals, with an accuracy of not far from 1 per cent. The subsequent use of these carbon-dioxide measurements in computing the total energy transformations involves a most careful consideration of the fundamental data obtained by Professor Armsby upon the relationships between carbon-dioxide production, methane and direct heat measurements, data which can be secured only with the respiration calorimeter at the Institute of Animal Nutrition at State College, Pennsylvania.

## PULSE-RATE TECHNIQUE.

The customary locations for feeling pulses in cattle are the submaxillary artery at the point where it winds around the lower jawbone, the metacarpal artery on the back part of the fore fetlock, and the middle sacral artery underneath and near the root of the tail. However, considerable difficulty was encountered at each of these locations in obtaining count for a sufficient length of time to be of value. Some of the steers (Nos. 1 to 12) were rather nervous about being handled either at the jaw or the foot, so that they would disturb or break the count, after 5 or 10 beats were obtained, by sudden movements, and the pulse under the root of the tail was found to be so weak as to make the count uncertain. The problem was finally solved by taking the heart-beat directly with the use of a stethoscope placed on the chest underneath the foreleg, where continuous counts of over a minute could be obtained easily and without fail. The accuracy of taking the heart-beat by use of a stethoscope was checked by two individuals and found to be very satisfactory. The general method of procedure followed was to enter the stall slowly, patting the animal in order not to excite him, and after placing the stethoscope for the count of a minute, to repeat for two more minutes as a check. Notwithstanding the even tenor of existence with regard to feed and activity, small temporary variations were observed from day to day, since the heart-beat reacts apparently with a great degree of sensitiveness to all kinds of stimulations. It was, therefore, necessary to observe carefully whether the animal was eating or ruminating, and record such a fact, as well as to take care that he was not unduly excited either by the attendant, by flies, or any other worrying causes, such as the expectation of being fed or watered. It was also necessary to guard against taking pulses immediately after an animal had risen to his feet from a lying position, as any of these factors would be responsible for a very temporary increase of from 2 to 10 beats per minute. The time best suited for taking pulses, therefore, was about 10 a. m. for steers 1 to 12, after they had cleared up all the feed and about an hour before watering, and at 2 p. m. for steers A and B, just before watering and weighing.

## RECTAL TEMPERATURE TECHNIQUE.

Rectal temperatures were taken with clinical thermometers about 4 inches in length and of the type generally used by veterinarians in testing cattle for tuberculosis. These were on a Fahrenheit scale, of a very sensitive type guaranteed to record in one-half minute. Temperatures were usually taken at the same time as pulse-rates, the common method of procedure being to insert the thermometers before reading pulses, removing them after pulses were taken, i. e., in about 2 to 3 minutes, thus giving a good safety margin of time for the mercury to reach the maximum.

## SKIN-TEMPERATURE TECHNIQUE.

Measurements of skin temperature on these animals were made, but not at the beginning of the series of experiments, for it was not until the profound alteration in the basal metabolism was noted that it seemed that there might be possible disturbances of heat-loss through the skin. Meanwhile a technique for measuring accurately the skin temperature of humans had been developed at the Nutrition Laboratory[a] and extensively used. This technique, however, was based upon the necessity for securing the true skin temperature on the unexposed parts of the human body. With cattle, covered as they are with hair, the question of true surface temperature becomes considerably involved, and immediately one has to decide as to whether the temperature will be determined on the outside of the hair or at the base of the hair, directly next to the skin. The difficulties of securing surface temperature have been touched upon by many writers, and all attempts to better the technique have followed the general line of reasoning that the true surface temperature should be measured by an appliance not affected by the temperature of the environment, so that the measurement recorded is a true surface temperature and not a resultant of surface temperature and environmental temperature. As a result of this criticism, practically all of the methods for securing temperature by mercurial thermometers have to be ruled out. The application of a flat-bulb thermometer, with an unprotected side, to the skin simply results in the measurement of the skin temperature, on the one hand, and the environmental temperature, on the other. If, however, the mercurial thermometer is protected with some insulating material, there is immediately a retarding of the normal loss of heat from the skin and there is a local rise in temperature as a result of this insulating material. This particularly affects those observations where the thermometer with its insulating material is applied for some time, and hence this criticism affects a great deal of some of the more recent work. A number of very interesting discussions on skin temperature have appeared from the veterinary clinic of Gmeiner in Giessen.[b] But practically all observations are affected by the criticisms raised above.

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[a] Benedict, Miles, and Johnson, Proc. Nat. Acad. Sci., 1919, 5, p. 218.

[b] Dissertations by Boeckh, Unters. ü. d. Hauttemperatur d. Tiere, 1910; Marioth, Beiträge z. Kenntnis d. Hautwärme beim Hunde, 1910; Spoerl, Beiträge z. Kenntnis d. Hautwärme bei Pferd u. Rind, 1911; Knorpp, Unters. ü. d. Hauttemperatur bei d. Ziege u. beim Schafe, 1911; Baumeister, Beiträge z. Kenntnis d. peripheren Temperatur bei Pferd u. Rind, 1912; Engel, Die Beeinflussung d. Hauttemperatur durch Verlust d. Haarkleides, 1912; Junginger, Unters. ü. d. Einfluss d. Wärmezufuhr auf d. Hauttemperatur bei Pferd u. Rind, 1912; Grether, Beeinflussung d. Hauttemperatur d. Rindes durch Frottieren, 1913.

From experience on humans it is quite clear that the thermo-junction method is about the only one available for giving true skin temperatures, but even this demands special consideration in the application of the junctions. The most recent use of this method for the temperature of ruminants is that of Wood and Hill in England.[a] For our own work we employed the thermo-junction method, keeping the constant-temperature junction in a vacuum bottle with a carefully calibrated tenth-degree thermometer, and taking the differential readings on a small portable galvanometer. While in general the junction was laid directly upon the surface of the skin, that is, at the outer surface of the hair, in certain tests the bare junction was laid directly on the skin at the hair roots. It is believed that the readings are correct to within 0.2° C.

## BARN-TEMPERATURE RECORDING INSTRUMENT.

Barn-temperature records were taken with a continuous recording instrument made by Richard Frères (Paris). An ordinary mercurial thermometer (standardized centigrade) was kept on the shelf with the instrument and the readings were checked from time to time, primary adjustment having first been made on the basis of the mercurial reading. Subsequent readings of the two checked to within 1° C.

## PHOTOGRAPHY.

As the best method for visualizing these animals at their different planes of nutrition, we relied upon photographic records. At various stages of progress the animals were photographed standing on a platform in characteristic poses and as nearly as possible under the same conditions, so as to make the photographs comparable. The attempt was made to have a 2-meter stick hanging directly over the backbone of the animal, so as to put upon the photographic record a scale to which measurements might be referred. This was done primarily with the view of possibly determining by a photographic method the surface area of these animals, somewhat on the principle for determining the surface area of humans outlined by one of us in an earlier paper.[b] The photographs, furthermore, give a good indication of the general appearance of the animals as time progressed.

Although impossible of reproduction, yet as a permanent record in the Nutrition Laboratory archives of the physical condition of these animals at the end of their long period of undernutrition, several hundred feet of motion picture film were made. Since with the projection apparatus the time of projection is reasonably uniform, and hence no great error in the time required for projection is introduced, these films give an astonishing indication of the general physical activity of these animals at this time. No phraseology can possibly describe adequately their appearance. It is only to be regretted that the technique for the projection of motion-picture films is not universal, as readers are deprived of the possibility of seeing these animals in motion. They moved about the exercise yard with a freedom and speed wholly unexpected; one animal actually jumped over the fence, and several engaged in strenuous horn-locking episodes.

[a] Wood and Hill, Journ. Agric. Sci., 1914, 6, p. 252.
[b] Benedict, Am. Journ. Physiol., 1916, 41, p. 275.

# CHRONOLOGICAL HISTORY OF THE RESEARCH.

To give a general idea of the research and the sequence of events, a chronological history is included here for the periods of observations both with steers 1 to 12 and with steers A and B.

## OBSERVATIONS WITH STEERS 1 TO 12, INCLUSIVE, 1918–1919.

Nov. 12. Steers 1 to 12 purchased. Until November 27 fed on hay (amount not recorded) and allowed the run of a small pasture, where they could get but little grass.

Nov. 18 to 28. Installation of respiration chamber at Agricultural Experiment Station, Durham, New Hampshire; apparatus tested and made ready for use.

Nov. 23. First records of body-weights; body-weights recorded daily, with but few exceptions, through November 4, 1919.

Nov. 27. First daily records of hay consumed.

Nov. 27 to Dec. 21, inclusive. Preliminary feeding period (with hay alone) to establish maintenance requirements, based on body-weights, Group II (steers 1, 3, 7, 10, and 11) and Group III (steers 6, 8, 9, and 12).

Nov. 27 to Dec. 27, inclusive. 31-day period on hay maintenance rations, control Group I (steers 2, 4, and 5).

Dec. 3. First respiration experiment made (with steer 3).

Dec. 14. First daily record of temperature in barn.

Dec. 15. First records of rectal temperature; measurements not made daily but at very short intervals of time.

Dec. 17. First set of photographs of steers taken, showing side and rear views; also photographs of respiration chamber and absorber table.

Dec. 18. First daily records of pulse-rate.

Dec. 20. First record of body measurements (length of trunk, depth, width, and circumference of chest, etc.). These measurements made, not daily, but at rather long intervals.

Dec. 22 to 27, inclusive. Preliminary feeding period on approximately 50 per cent maintenance hay rations, Group II (steers 1, 3, 7, 10, and 11).

Dec. 22 to Feb. 7, inclusive. Period on 66 per cent maintenance hay rations, Group III (steers 6, 8, 9, and 12).

Dec. 28 to May 5, inclusive. Maintenance hay rations, Group I.

Dec. 28 to May 5, inclusive. Main feeding period on 50 per cent maintenance hay rations, Group II.

Feb. 6. First daily observations of position of steers, i. e., whether lying or standing. Four observations made each day to November 4, 1919.

Feb. 6. First daily records of amount of water consumed.

Feb. 8 to May 5, inclusive. Period on 40 per cent maintenance hay rations, Group III.

Feb. 8. Up to this date evening feed prior to a respiration experiment withheld, but animal received 2.5 pounds hay (1.13 kg.) just before entering respiration chamber; after this date animal received no hay 24 hours before entering chamber.

Apr. 23. Comparison of metabolism standing and lying, steer 3.

May 1. Comparison of metabolism standing and lying, steer 3.

May 3. Second set of photographs taken, showing side and rear views of steers.

May 4 to 6, inclusive. Visit of and conference with Professor Henry Prentiss Armsby, of the Institute of Animal Nutrition, State College, Pennsylvania. At this time a photograph taken of Professor Armsby and motion pictures taken of steers.

May 5. Series of skin temperature measurements made, on this date only.

May 5 and 6. 48-hour fasting experiment with steer 1.

May 6 to 12, inclusive. Groups II and III fed back to full maintenance rations (hay only); Group I still on hay maintenance rations.

May 6. Second record of body measurements (length of trunk, etc.).

May 8 and 9. 48-hour fasting experiment with steers 4 and 10.

May 11. First *daily* records of chest circumferences; measurements made daily through November 3, 1919.

May 13 to Aug. 27, inclusive. Group I, fattening period. Steers 4 and 5 on mixed rations of hay and grain (steer 4 on high-protein rations, steer 5 on low-protein rations). Steer 2 fed on hay alone through May 19; put on pasture May 20 to August 27, inclusive; received no grain at all.

May 13 to Nov. 3, inclusive. Groups II and III, fattening period. Steers 1, 7, and 11 on mixed rations of hay and grain (low protein). Steers 3, 8, and 12 on mixed rations of hay and grain (high protein). Steer 10 fed back on hay alone from May 13 to July 7, inclusive, and fed both hay and grain (high protein) from July 8 to Nov. 3, inclusive. Steers 6 and 9 on pasture, May 13 to Oct. 28, inclusive, during which time they also received hay (May 13 to 16, inclusive, and Oct. 5 to Nov. 3, inclusive); taken off pasture Oct. 29, and given grain (October 29 to November 3, inclusive).

May 23. Last daily record of temperature in barn.

June 7. Third set of photographs taken, showing side and rear views of steers.

July 1 and 2. 48-hour fasting experiment with steer 4.

July 5. Third record of body measurements (length of trunk, etc.).

July 14 and 15. 48-hour fasting experiments with steers 9 and 11.

July 25. Last records of rectal temperature.

Aug. 7. Fourth record of body measurements (length of trunk, etc.).

Aug. 27. Photographs taken of Group I, side and rear views.

Aug. 28. Group I (steers 2, 4, and 5) slaughtered. Photographs taken of different views of carcasses.

Oct. 14. Photographs of Groups II and III, side and rear views.

Oct. 22. Comparison of metabolism standing and lying, steer 8.

Oct. 23. Comparison of metabolism standing and lying, steer 11.

Oct. 27 and 28. 48-hour fasting experiments with steers 6 and 7.

Oct. 29 and 30. 48-hour fasting experiments with steers 1 and 3.

Oct. 31. Last respiration experiments (with steers 8 and 12).

Nov. 2. Last records of pulse-rate and chest circumference.

Nov. 3. Last daily records of water consumed.

Nov. 4. Last body-weight measurements.

Nov. 6. Fifth and last record of body measurements (length of trunk, etc.).

Nov. 11. Group II (steers 1, 3, 7, 10, and 11) and Group III (steers 6, 8, 9, and 12) slaughtered. Photographs taken of different cuts of carcasses.

## OBSERVATIONS WITH STEERS A AND B, 1919–1920.

Nov. 14. Steers A and B (Group IV, purchased Nov. 1) brought to Durham.

Dec. 15 to 27. Preliminary feeding period, hay only, to determine approximate maintenance requirements.

Dec. 27 to Jan. 10. Each day begins and ends at 2 p. m. At 2 p. m., Dec. 27, period 1 on maintenance hay rations begun. Animals weighed daily at 2 p. m., at beginning and end of each 24 hours and before and after watering; fed at $4^h45^m$ p. m. and $6^h30^m$ a. m. (except when feed was withheld on account of a respiration experiment). Feces and urine collected at end of 24-hour period. Pulse taken just before end of 24-hour period and before animals had water.

Jan. 3. First daily record of temperature in barn.

Jan. 7 and 8. First respiration experiments with both steers A and B, 48 hours fasting.

Jan. 10 to May 29. Periods 2 to 11, inclusive, on 40 per cent maintenance hay rations.

Jan. 21. First rectal temperature measurements; measurements made at rather long intervals through December 16.

Apr. 6 and 7. A continuous 24-hour respiration experiment made with steer A (without feed).

May 17. Last daily record of temperature in barn.

May 29 to June 12. Period 12. Group IV fed back with maintenance rations (hay only).

June 5. First records of body measurements (length of trunk, depth, width, and circumference of chest, etc.).

June 12 to Oct. 15. Group IV on pasture.

Sept. 15, 16, and 17. Comparison of metabolism standing and lying, steer B.

Oct. 15 to 22. Group IV fed on hay (amount not recorded).
Oct. 22 to Dec. 17. Periods 13 to 16, inclusive. Group IV receive fattening rations of hay and grain (low protein, steer A; high protein, steer B).
Nov. 5. Second record of body measurements (length of trunk, etc.).
Nov. 29. Measurements of chest circumferences.
Dec. 14, 15, and 16. Measurements of chest circumferences.
Dec. 16. Last records of rectal temperatures.
Dec. 17. Last pulse-rate records, last records of urine and feces excreted, feed consumed, and water drunk.
Dec. 18. Last respiration experiments; also last records of body-weight.
Dec. 21. Third and last record of body measurements (length of trunk, etc.).
Dec. 21. Steers A and B slaughtered.

# DISCUSSION OF RESULTS.

## LIVE BODY-WEIGHT.

The body-weight of animals has particular economic significance, because it is upon the basis of live weight that meat animals are usually sold. While body-weight is practically and often scientifically accepted as the most convenient and reliable index to quantitative changes in body-tissue, yet there occur artificial fluctuations of great magnitude, caused by factors wholly extraneous to the deposition or loss of organized tissue that render body-weight records of only a general value and scientifically very misleading. Consequently, an examination of the normal body-weight and the fluctuations therein has an economic as well as physiological interest. Daily fluctuations of 2 or 3 pounds in the weight of the human body,[a] although often assumed to be an important index to change in tissue, have really but little, if any, significance in this respect, since the large proportion of water existing in the tissue of the human body (somewhat over 60 per cent on the average) may naturally be drawn on or added to in no small measure without any change whatsoever in the actual amount of organized tissue. With a steer whose weight is six to eight times that of the average man, we may upon this basis alone expect variations of 20 to 25 pounds in weight, which would be of no great significance. However, in a full-grown steer daily fluctuations even greater than this actually do occur, a condition which one might anticipate from a close study of the comparative intestinal physiology of the ruminant and of the nonruminant.

### Factors Affecting Body-weight.

Considering the body as the recipient of varying amounts of food and drink and the feces, urine, and insensible perspiration as the seepage and evaporation from the reservoir, the actual weight at any given time will be in large part dependent upon the ratio between ingesta and egesta, provided no additions to or drafts upon the organized body-tissue are made. Indeed, on this basis one could approximately predict body-weight, knowing the weight of ingesta and egesta. Such simple conditions do not exist, however, for, in addition to the factors of ingesta and egesta, there occur the losses due to variation in exercise and metabolic activity which must be considered. But of even greater significance is the fact that the animal body may retain relatively large masses of undigested or, indeed, partly digested feed, accompanied by large volumes of water.[b] This mass, commonly termed "fill," is equally prone to a decrement when the feed is reduced, and thus the factor of a widely varying weight of fill is ever present.

The really important factors that cause disturbing, artificial weight fluctuations are, therefore, of an external nature so far as they relate to changes in the actual mass of body-tissue, and precise knowledge of their relative

[a] Consideration need hardly be given here to those great losses in body-weight resultant upon severe muscular exercise, when, for example, 6.4 kg. may be lost in a 1-hour football game. (See Benedict and Joslin, Carnegie Inst. Wash. Pub. No. 176, 1912, p. 96, Table 114.)

[b] With ruminants large amounts of sand eaten with roughage may be stored in the alimentary tract. Zuntz and his associates (Landw. Jahrb., 1913, **44**, p. 776) noted a plus balance of from 2 to 3 kg. of silicic acid ascribable to the sand in beet leaves eaten in a previous experiment. They also write of necropsies showing large sand deposits in the digestive tract of herbivora.

influences on fluctuations of live weight becomes a matter of primary importance. While of these factors the ingesta can, in a sense, be directly controlled, this is only partially true, as illustrated by the old proverb that "you can lead a horse to water but you can not make him drink." The excreta are only indirectly and, indeed, very remotely controllable as a natural consequence of regulated alterations in the *amount* of feed and drink. But of far greater import in establishing the actual body-weight (i. e., weight uncontaminated by variable weights of fill) is the *character* of the feed, for even with humans[a] it has been shown that the change from a predominantly fat diet to one containing a large proportion of carbohydrates (but with equal calorific value) can easily result in the retention or addition of 800 to 900 grams of water per day for several days. Thus, in addition to the changes in the solid matter of fill, there may be specific effects upon the water-storage in the body-tissues.

Since it is recognized that daily fluctuations in live weight of tissue are relatively small and that daily fluctuations in the transitory ballast (i. e., ingesta and excreta) may be of such magnitude as to disguise entirely the quantitative tissue changes, it becomes of extreme importance here to establish an approximate relationship between exchanges in ballast, on the one hand, and live-weight fluctuations, on the other hand, and especially to establish the range for normal fluctuations where the ingesta is constant over a long period of time. With steers (particularly with steers under the conditions of study in this research up to the period when realimentation begins) the exercise and the character of the ingesta may remain essentially constant, and yet the amount of water consumed and the amounts of feces and urine excreted may vary materially.

The normal fluctuations to be expected with a steer under ordinary, yet constant, conditions of feeding are rather considerable. Armsby[b] has given this subject extended discussion, based on his vast experience. He cites a typical illustration in which a steer, fed on a uniform ration of 6.35 kg. of timothy hay and kept under as uniform conditions as possible, showed a variation in weight ranging from 418.6 to 444.8 kg. in 11 days. Since the exercise must have been very uniform and the character of the feed was uniform, it is clear that these fluctuations must have been due primarily to variations in the amount of water drunk, the amount of excreta, or both. During a large part of our own research, as was the case in Armsby's experiment, the exercise and the character of the feed given were qualitatively and quantitatively constant, thus eliminating these two factors as material, causative agents in effecting live-weight fluctuations. Of the two remaining factors, namely, weight of water intake and weight of excreta, it is not only important to determine which plays the greater rôle, but it is also important to determine the extent to which the plane of nutrition influences, quantitatively, these two factors. Fortunately, our experiments with Group IV lend themselves to a discussion of these last two points, as the live weight, the amount of water consumed, and the amounts of urine and feces passed were determined carefully each day.

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[a] Benedict and Milner, U. S. Dept. Agric., Office Expt. Sta. Bull. 175, 1907, p. 225; see also Benedict and Joslin, Carnegie Inst. Wash. Pub. No. 176, 1912, p. 92.

[b] Armsby, Bull. 42, Agric. Expt. Sta., Pa. State College, 1898, pp. 73 and 176; *ibid.*, Nutrition of farm animals, New York, 1917, p. 197.

### COMPARISON OF DAILY FLUCTUATIONS IN WEIGHT OCCURRING ON DIFFERENT FEED-LEVELS.

Since all of our animals were fed approximately maintenance rations for about 2 to 3 weeks before any changes in feed were made, data were obtained which permit a study of the variations in the weights on this feed-level and a comparison of these variations with fluctuations that occurred on other rations. The results are summarized in Table 8, which gives the average live weights and the ranges in daily weights of each steer during three short, selected periods, the first representing the last 2 weeks on maintenance, the second the last 2 weeks on submaintenance, and the third the last 2 weeks on fattening rations. These periods were selected as representative phases of the various feed-levels and are combined in this table for the purpose of comparing live-weight fluctuations under these different feed conditions. In preparing this table it has been recognized that certain unavoidable factors in the technique of the respiration experiments interfered with these body-weight records—that is, on certain days the animals were studied inside a respiration chamber and the night before their feed had accordingly been withheld, which might tend to make a minimum weight on the morning of the respiration experiment. Furthermore, on the morning after the respiration experiment, since the feed had been reduced during the day before, there might also be a tendency for a minimum weight. Hence, in tabulating these variations in weight, we have avoided any minimum weights occurring on the mornings of the days upon which respiration experiments were made or on the mornings of the days after respiration experiments were made. Similar care has been exercised to avoid the influence of any "make-up" feeds upon the maximum weights. Thus we believe we have completely eliminated the disturbing factor of the temporary withdrawal of feed at the time of respiration experiments.

The first (supposedly maintenance) period selected for our comparison extended with steers 1 to 12 from December 9 to 22 and with steers A and B from December 27 to January 10. The range in live weights during this period varies from a minimum of 9 kg. with steer 12 to a maximum of 26 kg. with steer 10. Since the animals of Group I were not subjected to ration curtailment, their weight ranges during the second period, April 21 to May 5, represent a feed condition approximately comparable to that in the first maintenance period of December 9 to 22. The weight ranges are from 12 kg. with steer 2 to 25 kg. with steer 5, values quite in line with those found with the other groups prior to ration curtailment. In general, then, adult animals on a maintenance hay ration, with water *ad libitum*, show a range in daily weights which may amount to as much as 20 or even 26 kg. With these steers both the exercise and the feed were uniform, and hence it is clear that we have to deal here with fluctuations due primarily to changes in the amount of water drunk and the amount of feces and urine passed.

With considerably less feed per day will animals exhibit proportionally as great weight variations? Since a pronounced loss in body-weight and a material reduction in the amount of fill followed the ration curtailment, it is important to note the effect of the reduction upon the range in live weight and also upon the amount of reduction in fill. This latter point will be dealt with later in this discussion. With Groups II and III the period from April

21 to May 5, i. e., the end of the curtailed-ration period, was selected as representing the minimum of weight and fill. With steers A and B the period from May 16 to 29 was correspondingly selected. The ranges in weight during this period amount to a minimum of 6 kg. with steer 7 and to a maxi-

TABLE 8.—*Average body-weights and ranges in daily body-weights of steers on maintenance, submaintenance, and fattening rations.*

| Group, steer, and date.[1] | Average body-weight. | Range in weight. | Difference. |
|---|---|---|---|
| Group I: | *kg.* | *kg.* | *kg.* |
| Steer 2—Dec. 9 to Dec. 22 | 458 | 451 to 466 | 15 |
| Apr. 21 May 5 | 446 | 442 454 | 12 |
| Aug. 12 Aug. 25 | 517 | 506 530 | 24 |
| Steer 4—Dec. 9 Dec. 22 | 521 | 517 527 | 10 |
| Apr. 21 May 5 | 495 | 492 505 | 13 |
| Aug. 12 Aug. 25 | 620 | 607 633 | 26 |
| Steer 5—Dec. 9 Dec. 22 | 605 | 594 611 | 17 |
| Apr. 21 May 5 | 587 | 580 605 | 25 |
| Aug. 12 Aug. 25 | 714 | 701 727 | 26 |
| Group II: | | | |
| Steer 1—Dec. 9 Dec. 22 | 581 | 574 587 | 13 |
| Apr. 21 May 5 | 457 | 449 462 | 13 |
| Oct. 21 Nov. 4 | 690 | 683 701 | 18 |
| Steer 3—Dec. 9 Dec. 22 | 500 | 489 508 | 19 |
| Apr. 21 May 5 | 383 | 378 389 | 11 |
| Oct. 21 Nov. 4 | 613 | 606 636 | 30 |
| Steer 7—Dec. 9 Dec. 22 | 461 | 443 467 | 24 |
| Apr. 21 May 5 | 353 | 351 357 | 6 |
| Oct. 21 Nov. 4 | 582 | 568 597 | 29 |
| Steer 10—Dec. 9 Dec. 22 | 589 | 575 601 | 26 |
| Apr. 21 May 5 | 456 | 448 463 | 15 |
| Oct. 21 Nov. 4 | 690 | 668 719 | 51 |
| Steer 11—Dec. 9 Dec. 22 | 519 | 510 525 | 15 |
| Apr. 21 May 5 | 385 | 366 395 | 29 |
| Oct. 21 Nov. 4 | 622 | 612 644 | 32 |
| Group III: | | | |
| Steer 6—Dec. 9 Dec. 22 | 434 | 422 439 | 17 |
| Apr. 21 May 5 | 342 | 337 347 | 10 |
| Oct. 21 Nov. 4 | 489 | 471 506 | 35 |
| Steer 8—Dec. 9 Dec. 22 | 472 | 465 479 | 14 |
| Apr. 21 May 5 | 342 | 332 351 | 19 |
| Oct. 21 Nov. 4 | 562 | 542 587 | 45 |
| Steer 9—Dec. 9 Dec. 22 | 570 | 562 580 | 18 |
| Apr. 21 May 5 | 454 | 450 458 | 8 |
| Oct. 21 Nov. 4 | 620 | 595 641 | 46 |
| Steer 12—Dec. 9 Dec. 22 | 401 | 398 407 | 9 |
| Apr. 21 May 5 | 292 | 285 297 | 12 |
| Oct. 21 Nov. 4 | 510 | 505 527 | 22 |
| Group IV: | | | |
| Steer A—Dec. 27 Jan. 10 | 600 | 596 608 | 12 |
| May 16 May 29 | 468 | 450 490 | 40 |
| Dec. 4 Dec. 17 | 681 | 665 691 | 26 |
| Steer B—Dec. 27 Jan. 10 | 567 | 562 580 | 18 |
| May 16 May 29 | 443 | 428 460 | 32 |
| Dec. 4 Dec. 17 | 663 | 655 675 | 20 |

[1] With Groups II, III, and IV, Dec. 9 to 22 and Dec. 27 to Jan. 10 represent periods on maintenance rations; Apr. 21 to May 5 and May 16 to 29, submaintenance rations; Oct. 21 to Nov. 4 and Dec. 4 to 17, fattening rations. With Group I, Dec. 9 to 22 and April 21 to May 5 represent periods on maintenance rations; Aug. 12 to 25 represent periods on fattening rations for steers 4 and 5, and pasture period for steer 2.

mum of 40 kg. with steer A. In this period of submaintenance feeding, therefore, the range is actually wider than on maintenance feeding and, what is of greatest importance, the maximum value of 40 kg. with steer A is 14 kg. greater than the maximum range of 26 kg. noted in the maintenance period with steer 10.

During the last period, when the heavy fattening rations were given to each group, it is not surprising that in general the widest variations in weight are noted with nearly every animal. Special interest lies, therefore, in a close analysis of the weight ranges in the first and second periods, i. e., the maintenance as compared to the submaintenance period, in which it will be remembered that approximately but one-half the weight of hay was given these animals.

Such an analysis is best made on average values, and we have accordingly given in Table 9 the average range in weight during each of the main periods, (i. e., maintenance, submaintenance, and fattening) for each group of animals.

TABLE 9.—*Average range in daily weight of groups of steers on maintenance, submaintenance, and fattening rations.*

| Group. | Average range in weight during last 2 weeks.[1] | | |
|---|---|---|---|
| | Maintenance. | Submaintenance. | Fattening. |
| | *kg.* | *kg.* | *kg.* |
| I | 14 | [2]17 | 25 |
| II | 19 | 15 | 32 |
| III | 15 | 12 | 37 |
| IV | 15 | 36 | 23 |

[1] See Table 8 for dates selected for the 2-week periods.

[2] This range in weight for Group I was observed at the end of their *maintenance* feeding period, and is included in this column simply because it represents the same dates selected for Groups II and III on *submaintenance.*

Thus, in the control group the average range during the first period for all three animals is 14 kg., during the second period 17 kg., and during the third 25 kg. In two of the four groups, namely, Groups I and IV, the average range is larger in the second period than in the first, while in the other two groups the condition is the reverse. With Groups II and III, that were upon distinctly submaintenance rations in the second period, there is evidence of a slightly smaller range in the weight, and these two groups alone would speak for a lowered variability upon the lower nutritive level. In striking contrast to this, however, is the extraordinary range observed with steers A and B during the submaintenance period. The fact that this range of 36 kg. is even greater than that observed in the subsequent heavy feeding period makes it impossible to draw any general conclusion with regard to the influence of the lower nutritive level upon the average range in weight. With the animals 1 to 12 the large weight variability noted in the fattening period is readily explainable as the result of the heavy feeding. The anomaly of the greater weight variation appearing with steers A and B on the submaintenance ration rather than with the fattening ration, as was the case with the other animals, is subsequently explained (see p. 111).

It seems perfectly clear from an analysis of the data in Tables 8 and 9 that the low submaintenance period has little, if any, effect upon the normal range in weights, save in the case of steers A and B, where a large increase in this range is found, in spite of a very marked loss of body-weight amounting to about 130 kg. with each steer.

In a series of experiments where the food conditions remain constant, as is the case in each of these periods, where activity is uniform, and where these large variations in weight still occur, it is obvious that one must look more carefully into the two other factors, i. e., water consumption and excreta, that might affect weight changes, for alterations of from 40 to 45 kg. within a 2-week period can hardly be ascribed to the loss of or deposition of organized body-tissue. Is it possible that irregularity in water intake, especially with uniform feed and exercise, might be responsible for these large fluctuations in weight? Different types of rations apparently have different effects on live-weight fluctuations, in part due to their influence on water consumption. On heavy grain rations the feed and feed residues must be of a more transitory nature than on hay rations. Heavy grain rations induce a larger water intake, which is much more uniform from day to day than with hay rations. This causes more uniform flushing, as is evident from the condition of the feces. On maintenance and particularly submaintenance rations with hay only there is a tendency for a greater irregularity in daily water intake, some of our animals having gone 2 days without drinking, a fact never observed on fattening. This would certainly tend to produce live-weight fluctuations. With two of our animals, A and B, data are fortunately at hand for making a more subtle analysis of the body-weight changes in this connection.

## RELATION BETWEEN DAILY WEIGHTS OF FEED, WATER, URINE, FECES, AND DAILY BODY-WEIGHTS.

In discussing weight variations, under conditions when the food remains essentially constant, it is important to distinguish clearly between those major changes in actual organized body-tissue due to prolonged periods of alteration in ration and those relatively short fluctuations in live weight, noted from day to day, due to changes in ballast and water-content. To analyze somewhat more closely the various factors which may enter into the changes in body-weight, we have plotted in Figs. 17 and 18 for steers A and B, respectively, the body-weights as well as the weights of water drunk, feed eaten, and feces and urine passed during 14 days (March 7 to 20, inclusive) on an essentially constant submaintenance ration.[a] Body-weights are recorded for the beginning and ending of each day, the time of weighing being 2 p. m. on any given date. The weights of feed and feces are indicated on the charts as being midway between the two dates. Thus, in Fig. 17 the body-weight of steer A at 2 p. m. on March 7 was 528 kg. During the suc-

[a] The data from which these charts were prepared were collected before the full significance of the insensible perspiration was recognized. Unfortunately, if the insensible perspiration is computed from these data, gross irregularities are noted on different days, irregularities that subsequent experimenting with similar animals (in which extraordinary precautions were taken with every weighing) shows do not exist. For the main purpose of our discussion, however, we still think it best to present the charts as shown, although disclaiming extreme accuracy for the computation of the insensible perspiration.

ceeding 24 hours the animal had 6,000 grams of hay and passed 5,460 grams of fresh feces and 2,270 grams of urine. At 2 p. m. on March 8 the body-weight had fallen to 518 kg.

The curves in Fig. 17 and particularly in Fig. 18 show a rather frequent relationship between large volumes of water drunk and increase in weight. That is, on days when no water was taken, or taken only in small amounts, such as on March 7–8, 9–10, 12–13, 16–17, 18–19, and 19–20 with steer A and March 8–9, 9–10, 11–12, and 15–17 with steer B, there was, as a rule, a distinct tendency for the body-weight to fall off, and the reverse is true when large amounts of water were consumed. However, this is not invariably the case, since on March 14–15 the body-weight of steer A actually increased somewhat in spite of the decreased water intake, but in general the

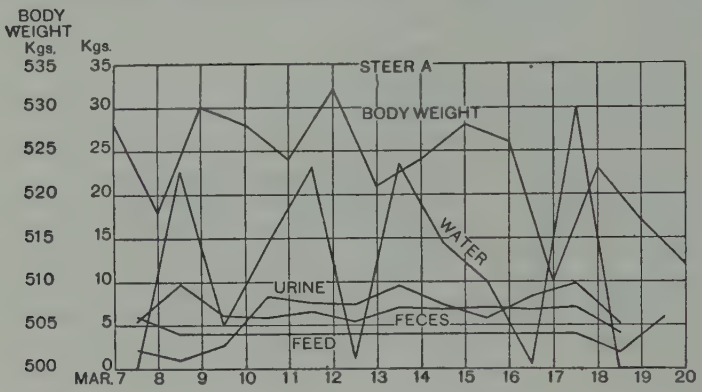


FIG. 17.—Curves for body-weight, water intake, urine and feces excretion, and feed consumption during 2 weeks on an essentially constant submaintenance ration of hay alone, steer A.

relationship is so striking as to make it perfectly clear that the gross fluctuations in body-weight are concurrent or reasonably so with gross changes in water consumption. It is important to note, likewise, that with steer A and, to a certain extent, with steer B, under this ration condition water ingestion was reasonably rhythmical, that is, days when large amounts of water were drunk alternated with days when little or no water was consumed.

Finally, an examination of the feces excreted fails to show a close correlation between such excretion and decreases in either body-weight or volume of water drunk, although it is to be noted that when the weight of feces increases one would normally expect a relative decrease in the subsequent body-weight, unless more than compensated by changes in water consumption. Similarly, the changes in the volume of urine are in no sense parallel to the changes in body-weight or the changes in water consumption, although not infrequently when water is taken sparingly the volume of urine falls off, and with steer B, where unusually large volumes of water were taken, the urine in several instances does show an increase in volume, but in no sense proportionate to the water consumed.

From these charts it is, therefore, clear that the major factor influencing gross fluctuations in body-weight from day to day is water consumption, and

that while on the one hand the weight of feces and weight of urine are not unaffected by the water consumption, and on the other hand are not without influence upon changes in body-weight, yet they play but a relatively minor rôle. A special study of the total water consumption and the factors affecting it is therefore necessary. Such treatment is given our data on page 112.

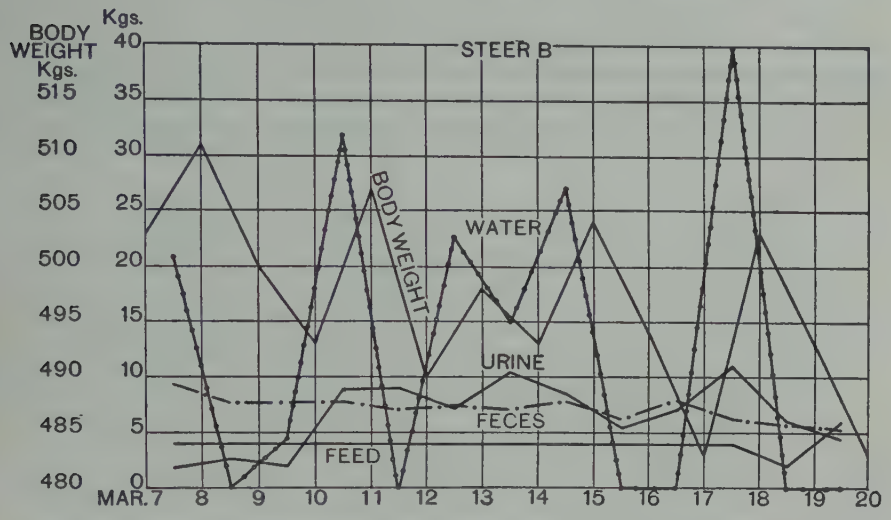


FIG. 18.—Curves for body-weight, water intake, urine and feces excretion, and feed consumption during 2 weeks on an essentially constant submaintenance ration of hay alone, steer B.

## MAJOR CHANGES IN BODY-WEIGHT DUE TO QUANTITATIVE VARIATIONS IN RATION.

In the foregoing discussion, emphasis has been laid upon the variations in weight noted from day to day, which are due primarily to alterations in the amounts of drinking-water consumed, although in all probability these live-weight variations are also influenced somewhat by daily changes in feed. These fluctuations have to deal with the day-to-day changes in weight, which were readily noted throughout the winter to be of considerable magnitude, even under conditions of constant ration.

We have now to consider the permanent changes in body-weight produced by marked, prolonged alterations in rations, specifically, in our research involving reduction in feed. A careful distinction, therefore, must be made between the analysis of weight changes of a transitory nature, due primarily, as is seen above, to changes in water consumption and general internal ballast and the analysis of prolonged, persistent changes in weight due to loss of organized tissue as a result of restriction in feed. For this latter analysis we have in our several groups of animals an admirable basis for discussion, since three of the steers were maintained as control animals on a normal feed basis, and hence the changes in weight noted with these three animals will give us some hint as to the variations to be expected when total body-weight is affected by factors other than changes in rations.

BODY-WEIGHT CHANGES OF THE CONTROL ANIMALS, GROUP I.

Steers 2, 4, and 5 were maintained as control animals—that is, throughout the winter they were given enough hay to hold them as near a uniform weight as possible. Furthermore, they were kept under substantially the same conditions as regards stall activity. We therefore have to deal here primarily with a proportionality between feed-intake and body-weight. During the first month these animals received exactly the same treatment as was given the other animals during their first, i. e., maintenance, period, and during this time they underwent no material changes in weight, as is shown from the curves in Fig. 19, which are plotted on the basis of 7-day averages of the weights. (In this and the three following charts, Figs. 20 to 22, the times of

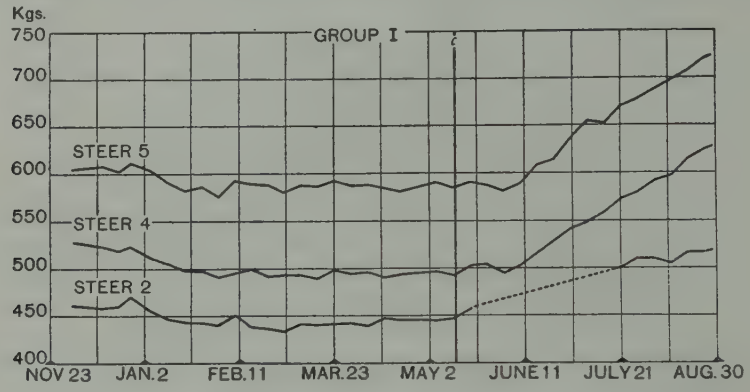


FIG. 19.—Body-weight curves of steers 2, 4, and 5, Group I.
The vertical line *c* represents the point at which the steers no longer received a maintenance ration of hay only, but began to receive a fattening ration of hay and grain. Steer 2 was on pasture after May 19.

changes in feed are indicated by heavy vertical lines.) During the latter part of December and for the next 2 months there was a distinct tendency for all three control animals to fall off somewhat in weight, the average total loss approximating not far from 30 kg. for each steer, the minimum weight being reached about the first of February. From there on the body-weights remained essentially at a constant level until about the middle of May, or at the period when grain was added to the ration for fattening. The cause of the loss in weight during the first part of the year, i. e., from December 27 to about February 1, is a little difficult to explain,[a] save on the ground that the ration for the month of January was a little too low for maintenance and that, in common with many other feeding experiments, the body-weight fell off slightly until the hay ration sufficed for maintenance, when it remained fairly constant until March 13, at which time a slight increase in feed (about 400 grams of hay per head) was given to all three animals. This slight increase in hay was not, however, perceptibly reflected in the course of the

[a] Trowbridge, Moulton, and Haigh (Univ. Missouri, Agric. Expt. Sta. Bull. 18, 1915, p. 34) state "Does a beef animal accustom itself to a low plane of nutrition so that the cost becomes less and less? The feeder who has had any experience knows that he has found it necessary in maintenance trials to repeatedly cut the feed in order to keep the animal from gaining weight."

body-weight curves, for they remained at essentially the same level until the fattening period began, on May 13.

Subsequent to May 12, steers 4 and 5 on the concentrate ration showed a marked, steady increase in weight, reaching their maximum weights in the last week in which records were obtained, when steer 5 weighed about 120 kg. and steer 4 about 100 kg. more than their initial weights. Steer 2 was turned out to pasture May 20 and weights were not obtained again until July 17. In these two months there was a distinct increase in weight, the animal weighing 40 kg. more on July 17 than he did at the start. The series of weights from this date to the end of the observations on August 28 show a still further moderate increase on pasturage, the final weight, however, being but 57 kg. greater than that at the beginning of the experimental work in the previous December.

Special attention, in Fig. 19, is called to the reasonably uniform body-weights throughout the first half of the year, for although the control animals lost somewhat, it is apparently a fairly regular loss. It is this section of the chart that has special value for comparison with the body-weights of the other groups of animals subjected to feed reduction. With special reference to the maintenance period, it can be seen from Fig. 19 that while our initial endeavor was to have the body-weights remain absolutely uniform throughout the entire winter, in this we were but partly successful, inasmuch as there was a slight fall from December 27 to February 1, as above noted, after which the feed was sufficient to hold the weight constant for the remainder of the hay period. The variability in weight, even with uniform feed and uniform muscular activity (stall conditions), is surprising. In this chart individual weights are not given, as all curves are based upon 7-day averages. Even within these 7-day averages there were variations in weights from week to week comparable in a way with the day-to-day changes already discussed. Thus, with steer 5 about February 1 there was an increase in average weight from one week to the next of 16 kg., while steers 4 and 2 for the corresponding periods showed increases of 5 and 9 kg., respectively, from one week's average to the next. Such weight variability with constant conditions of feed and exercise accentuates the uncertain significance not only of individual weights but, indeed, averages obtained from seven consecutive daily weights.

## BODY-WEIGHT AS AFFECTED BY PRONOUNCED CURTAILMENTS IN RATIONS.

### Weight Changes on a Ration somewhat less than One-half of the Maintenance Amount, Group II.

A group of five steers (Nos. 1, 3, 7, 10, and 11), after being fed for approximately one month on a maintenance hay ration, were subjected to a cut in ration corresponding to somewhat over 50 per cent of their energy needs at maintenance, and they were held on this reduced ration for a period of approximately 4½ months. This was followed by a resumption of the original maintenance ration of hay only for one week, and then by a fattening period in which hay was liberally supplemented by concentrates. The body-weight curves for this group of animals are recorded in Fig. 20, the heavy vertical lines, as in Fig. 19, indicating the points at which material alterations in feed were made. During the maintenance period it is noted that there was an

actual decrease in weight in the case of all five steers, and hence the ration can not properly be spoken of as a maintenance ration. Since all rations were computed on the basis of 500 kg. of live weight (an allowance being thus made for different sizes of animals), we are somewhat at a loss to explain this decrease during the maintenance period. Although the loss was relatively slight, it was noted with all five animals of this group, and, furthermore, it was noted in similar degree with the animals in Groups III and IV. With the curtailment of ration there was an immediate fall in weight, which persisted throughout the entire period, the rate of decrease during the first month being much more marked than subsequently. It was not until the last 2 weeks of the low-ration period that constancy in weight was approximated. During the week of May 6 to 12, when the maintenance hay ration was resumed, there was an increase in the weight of all 5 animals, followed by a still larger increase with all 5 individuals on fattening rations.

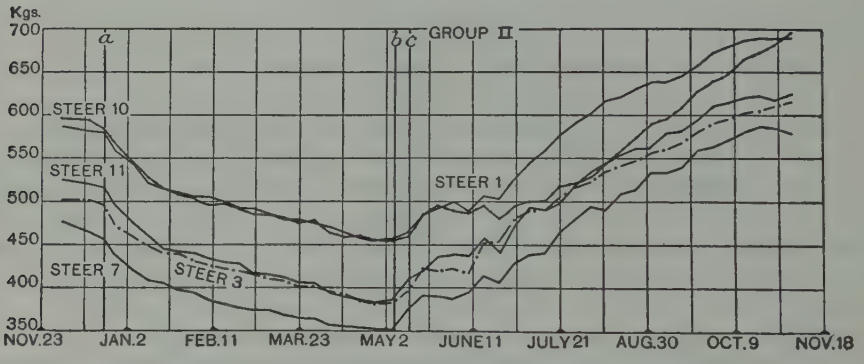


FIG. 20.—Body-weight curves of steers 1, 3, 7, 10, and 11, Group II.

The vertical line *a* indicates the end of maintenance period and the beginning of submaintenance period on hay alone; vertical line *b* indicates the beginning of 1-week period of realimentation with hay alone; the vertical line *c* indicates the beginning of the fattening period with hay and grain, except for steer 10, which received a maintenance ration of hay alone until July 8, and concentrates thereafter.

It is clear that the first half of these curves for Group II show a pronounced difference over the curves for the 3 control animals in Group I (aside from the slight loss noted with both groups during the so-called "maintenance" period), as all the curves for the steers in Group II show a great loss in weight throughout the period when the half ration was fed. In Table 10 are given the total and the percentage losses in weight for Group II and, for future reference, the number of days required on refeeding to regain the initial weight. The total losses range from 105 kg. with the smallest steer (No. 7) to 131 kg. with No. 11, which was somewhat larger than No. 7 but not so large as No. 1. This group of animals lost from 21 to 25 per cent of their initial weight in about 4½ months, with an average loss of 23 per cent.

The rate of loss was so noticeably different after the first month (constancy at the lowest level being reached during the last 2 weeks), that it is of interest to compare the exact percentages of total loss for the first month with those for the last 3 months, i. e., up to April 21. These data are accordingly given in Table 11. It is here seen that somewhat over one-half of the

loss took place during the first month of submaintenance feeding (i. e., up to January 22), and the rest occurred in the subsequent 3 months (i. e., up to April 21), weight constancy being attained during the last 2 weeks. The slope of the curve indicating the weight-loss for 3 months, from January 22 to April 21, is essentially a straight line in each case and represents on the average a weight-loss of 56 kg. in 3 months, or 19 kg. per month.

TABLE 10.—*Loss in weight on curtailed ration and time required to regain initial weight on refeeding, Group II.*

| Steer No. | Initial weight.[1] | Weight at end of reduction.[2] | Loss in weight. | | Days to regain initial weight on refeeding. |
|---|---|---|---|---|---|
| | | | Total. | Per cent. | |
| | *kg.* | *kg.* | *kg.* | | |
| 1 | 580 | 457 | 123 | 21 | 78 |
| 3 | 496 | 383 | 113 | 23 | 71 |
| 7 | 457 | 352 | 105 | 23 | 73 |
| 10 | 584 | 456 | 128 | 22 | [3]115 |
| 11 | 517 | 386 | 131 | 25 | 82 |

[1] Average weight for Dec. 16 to 22, prior to reduction.
[2] Average weight for April 28 to May 5.
[3] Steer 10 received only a maintenance ration of hay for 56 days and subsequently was fed hay and concentrates.

An analysis of the character of the loss is deferred until the weight curves of Groups III and IV are considered. It is somewhat significant that constancy at the lower weight-level was reached at about the same time with the entire group. It should be stated that the date for beginning to refeed was decided upon before this level of weight constancy was reached. It is fortunate that refeeding did not begin 3 weeks earlier.

With refeeding the general upward sweep of all the weight curves is at first sight essentially uniform. Since these animals were subjected to somewhat different treatment for fattening, steers 1, 7, and 11 being given a rather low-protein ration, and steers 3 and 10[a] a rather high-protein ration, further analysis of these weight increases during the fattening period should be deferred until the relationships between the protein intake and body-weight increases are considered.

### WEIGHT CHANGES WITH A 40 PER CENT CURTAILMENT OF RATION, FOLLOWED BY A FURTHER DECREASE, GROUP III.

A group of 4 animals, steers 6, 8, 9, and 12, were given substantially the same treatment as those in the preceding group, save that the curtailment in ration which followed the period of maintenance feeding was at first only about 40 per cent of maintenance rather than one-half. After 49 days on this ration an even greater curtailment followed (i. e., about 60 per cent), so that the animals were essentially on a ration amounting to only 40 per cent of that at the original level of weight maintenance. During the maintenance

[a] Steer 10 was at first given but a very small increase in hay, in an attempt to put him on a maintenance ration corresponding to his weight at that time. This ration was gradually increased, but consisted solely of hay until July 8. On that date he was given hay and grain (high protein).

period prior to the feed cut we note, as in the preceding group, an actual decrease in weight (see Fig. 21) with all 4 animals. With only 2 of them however, Nos. 8 and 9, were these decreases of mathematical significance. Since it is a fact that all 9 animals comprising Groups II and III, as well as steers A

TABLE 11.—*Loss in weight during the first month compared with the subsequent loss on a submaintenance ration, Group II.*

| Steer No. | Loss in weight. | | | Per cent of total loss occurring during— | | Loss per month during last 3 months. |
|---|---|---|---|---|---|---|
| | Total. | First month. | Last 3 months.[1] | First month. | Last 3 months. | |
| | *kg.* | *kg.* | *kg.* | | | *kg.* |
| 1 | 123 | 66 | 57 | 54 | 46 | 19.0 |
| 3 | 113 | 56 | 57 | 50 | 50 | 19.0 |
| 7 | 105 | 55 | 50 | 52 | 48 | 16.7 |
| 10 | 128 | 71 | 57 | 56 | 45 | 19.0 |
| 11 | 131 | 72 | 59 | 55 | 45 | 19.7 |
| Avg..... | 120 | 64 | 56 | 53 | 47 | 18.7 |

[1] Represents loss from Jan. 22 to Apr. 21, when constancy at the low weight-level was reached.

and B, showed a real, though in some instances slight, decrease in weight during the period of maintenance, we must call into question again our use of the word "maintenance" for this feed-level, as the ration was in all probability really somewhat below maintenance. Following the curtailment in ration, which with this particular group amounted at first to somewhat more than one-third of the original maintenance requirement, there occurred a decrease in body-weight (see Fig. 21) which proceeded with considerable regularity throughout this entire first period of ration curtailment, broken only by a slight, unexplainable increase for 3 of the animals about the latter part of January. With steer 9 the rate of loss in weight, as shown by the slope of the curve, was not materially greater than that actually observed during the maintenance period preceding it. On February 8 the rations were further reduced to approximately 40 per cent of the original maintenance amount, and the body-weight still continued to decrease, but singularly enough at a rate essentially that of the first period of reduction when they were getting somewhat more feed. This is more especially shown in the case of steer 6, which did not exhibit the slight rise in weight about the latter part of January.

An analysis of the weight curves along the lines followed in the preceding group of animals is difficult here on account of the fact that two successive curtailments in the amount of ration took place. Seemingly the weight had attained constancy toward the end of the first curtailment with 3 of the 4 animals (i. e., Nos. 8, 9, and 12), steer 6 alone continuing to lose weight to the end. With the further curtailment to 40 per cent of the original maintenance amount, the fall in weight was resumed with the 3 animals which apparently had struck a level, and continued at essentially the same rate with steer 6. For the last 2½ weeks of the period, namely, from April 16 to May 5, the weights may be said to have been constant, although 3 of the 4 animals

did show slight positive decreases. In any event, the regularity of loss was by no means that noted with Group II.

An analysis of the rate of loss in weight on the two submaintenance feed-levels is given in Table 12. By February 8 the animals had hardly lost much more than 10 per cent of their initial weight on the average. With the second, more drastic curtailment, the loss proceeded until they had lost from 20 to 27 per cent of their initial weight, this loss averaging for the 4 animals 24 per cent. The losses were quite irregular. Thus, the heaviest animal, No. 9, weighing 564 kg. prior to reduction, lost 111 kg., while a much lighter animal, No. 8, weighing 473 kg., lost 130 kg., and No. 12, which was 162 kg. lighter in

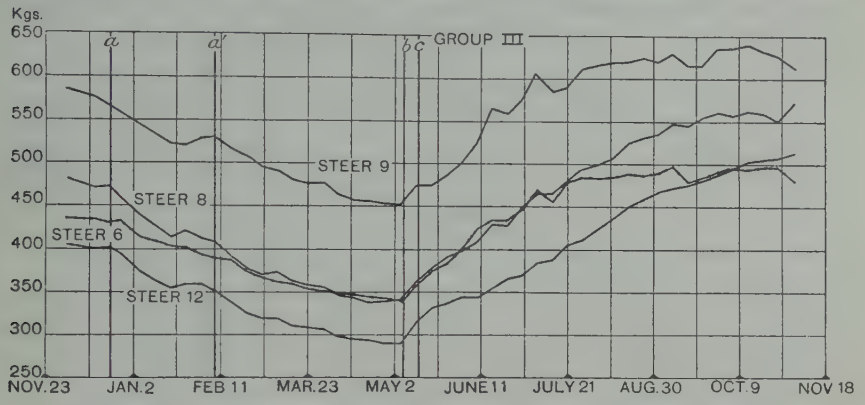


FIG. 21.—Body-weight curves of steers 6, 8, 9, and 12, Group III.

The vertical line *a* indicates the end of the hay-maintenance period and the point when the first curtailment in ration occurred, while *a'* indicates the point when the second curtailment in ration occurred. The vertical line *b* indicates the beginning of the 1-week period of realimentation with hay alone, and the vertical line *c* indicates the beginning of the fattening period with hay and grain for steers 8 and 12, and the beginning of the pasture period for steers 6 and 9.

weight than No. 9, lost essentially the same as No. 9. This irregularity in loss between the animals, it is to be noted, was not found in Group II. In consideration of the fact, however, that steer 9 lost a considerable amount during the maintenance period, it is possible that the loss in the submaintenance period simply represents a depletion from an already somewhat depleted body.

It is hardly feasible to determine here the rate of loss per month for comparison with the other groups, although after the second adjustment in ration for the 2 months from March 3 to May 5, inclusive, the weight curve for each steer is a reasonably regular line. But since there is a plateau from April 16 to May 5, the true fall can be measured only from March 3 to April 16. During this period of a month and a half (see Table 13) the loss ranged from 20 kg. with steer 6 to 38 kg. with steer 9, the average loss for the 4 animals being 28 kg., representing an actual average loss of 19 kg. per month. The important point, judged by this relatively short period, however, is that all 4 animals had essentially struck a level shortly after April 12, in which the balance between income and outgo must have been fairly well established.

On the resumption of hay maintenance rations, from May 6 to 12, all animals in this group showed an increase in weight, an increase which was

further augmented in the subsequent fattening period, both in the case of steers 6 and 9, which were fattened on pasture, as well as in the case of steers 8 and 12, which were fattened on grain and hay. After May 13, when steers 6 and 9 were put on pasture, their hay ration was gradually decreased until May 17, when no more hay was given. From October 5 on, these steers again received some hay in addition to the grass obtained on pasture, and on October 29 they were taken off pasture because of the cold weather and given hay and grain. (See Table 3 for details.) Analysis of these curves during the fattening period may properly be deferred.

TABLE 12.—*Loss in weight with two reductions in ration and time required to regain initial weight on refeeding, Group III.*

| Steer No. | Initial weight.[1] | At end of first reduction. | | | At end of second reduction. | | | Days to regain initial weight on refeeding. |
|---|---|---|---|---|---|---|---|---|
| | | Weight.[2] | Loss in weight. | | Weight.[3] | Loss in weight. | | |
| | | | Total. | Per cent. | | Total. | Per cent. | |
| | *kg.* | *kg.* | *kg.* | | *kg.* | *kg.* | | |
| 6 | 432 | 389 | 43 | 10 | 340 | 92 | 21 | 38 |
| 8 | 473 | 409 | 64 | 14 | 343 | 130 | 27 | 73 |
| 9 | 564 | 529 | 35 | 6 | 453 | 111 | 20 | 41 |
| 12 | 402 | 352 | 50 | 12 | 292 | 110 | 27 | 74 |

[1] Average weight for Dec. 16 to 22, prior to reduction.
[2] Average weight for Feb. 3 to 8.
[3] Average weight for Apr. 28 to May 5.

WEIGHT CHANGES IN TWO STEERS ON A RATION AMOUNTING TO 40 PER CENT OF THE MAINTENANCE REQUIREMENT, GROUP IV.

During the second year, i. e., the winter of 1919–20, we studied the body weights of 2 animals, steers A and B, under conditions of severe ration curtailment and confinement in metabolism stalls. The results are given in Fig 22. While the so-called "maintenance period" preceding the ration curtailment was relatively short with these animals, both showed, in common with essentially all of the other animals when on maintenance, a perceptible decrease in weight. On curtailment of the ration a more marked decrease in weight was found with steer A for about 3 weeks, while but little change was noted in the rate of loss with steer B. During the remainder of the submaintenance period the animals lost weight fairly regularly and at about the same rate. They were of nearly the same initial weight, lived under remarkably uniform external conditions such as stall activity, etc., and were given the same weight of feed. Since they remained in the metabolism stalls the entire time, it is not surprising that the body-weight curves are so uniformly parallel.

From May 29 to June 12 (period 12) the hay ration was again increased to the maintenance level, but the average amount consumed per day was somewhat greater than that consumed during the original maintenance period. In neither period, however, did the total daily average consumed amount to 9,090 grams (calculated maintenance), because of feed withheld for respira-

tion experiments. However, while steers A and B lost weight during period 1, on a similar feed-level during period 12 the body-weights rose instantly. Both animals were turned out to pasture from June 12 to October 15, and then brought back to the barn and fed unknown amounts of hay alone for a week, during all of which time no records of weight could be obtained. The body-weights, when finally secured again on October 22, were essentially at the same level at which they started at the beginning of the experiment. From October 22 to December 17 the steers were on fattening rations of hay and grain, but a difference was made in the character of the feed, steer A being given a low-protein ration and steer B a ration high in protein content. At the end of the year, when they were slaughtered, the animals had increased respectively 89 and 102 kg. above their initial weights. The losses in weight during submaintenance were 132 and 125 kg., respectively, for steers A and B, while the percentage loss was identical for the two animals, namely, 22 per cent.

TABLE 13.—*Loss in weight during the first month compared with the subsequent loss on a submaintenance ration, Group III.*

| Steer No. | Loss in weight. | | | Per cent of total loss occurring during— | | Loss per month March 3 to April 16, inclusive. |
|---|---|---|---|---|---|---|
| | Total. | First month.[1] | From March 3 to April 16, inclusive. | First month. | March 3 to April 16, inclusive. | |
| | *kg.* | *kg.* | *kg.* | | | *kg.* |
| 6 | 92 | 28 | 20 | 30 | 22 | 13.3 |
| 8 | 130 | 53 | 30 | 41 | 23 | 20.0 |
| 9 | 111 | 44 | 38 | 40 | 34 | 25.3 |
| 12 | 110 | 45 | 25 | 41 | 23 | 16.6 |
| Avg. | 111 | 43 | 28 | 38 | 25 | 18.8 |

[1]Represents loss from Dec. 22 to Jan. 22, inclusive.

Making allowance for the major changes which took place immediately after curtailment of ration, when about one-third of the weight was lost during the first month (see Table 14), we find that the rate of loss in weight subsequent to the first month was essentially the same with both animals, namely, 25 kg. per month, which was somewhat greater than the rate of loss noted with either Group II or Group III.

## INTESTINAL RESIDUE OR FILL AND ITS RELATION TO BODY-WEIGHT.

### EFFECT OF MAINTENANCE AND SUBMAINTENANCE RATIONS ON FILL.

It is quite clear from the individual body-weight curves that a very close relationship exists between the feed intake and the body-weight over long periods of time. At the beginning on the so-called "maintenance rations" practically all of the animals showed a slight fall in weight, implying that the assumed maintenance ration was not maintenance or that, having received more feed before the maintenance period was begun, the steers were slowly

losing some ballast and drinking less in proportion to feed intake. If, as a criterion of maintenance ration, one assumes uniformity or constancy in body-weight, this inference that the ration was not in reality maintenance ration is justifiable. If, however, one considers the proportion that exists between the feed-level and ballast, and the tendency for slow adjustment of the latter, then maintenance feeding should be carried over a longer period to prove that the ration does maintain constancy in weight, as was done with steers 2, 4, and 5.

TABLE 14.—*Loss in weight during the first month compared with the subsequent loss on a submaintenance ration, Group IV.*

| Steer No. | Loss in weight. | | | Percentage of total loss during— | | Loss per month. | |
|---|---|---|---|---|---|---|---|
| | Total. | First month. | Last 3⅔ months. | First month. | Last 3⅔ months. | Entire period. | Last 3⅔ months. |
| | *kg.* | *kg.* | *kg.* | | | *kg.* | *kg.* |
| A | 132 | 47 | 85 | 36 | 64 | 28 | 23 |
| B | 125 | 30 | 95 | 24 | 76 | 27 | 26 |

Changes in body-weight are essentially of two distinct types: (1) the transitory day-to-day changes, affected in large part by the volume of water consumed, and (2) the more persistent and prolonged increases or decreases, determined to a large extent by the character and particularly the amount of the ration. In considering the factors affecting these two different types of weight changes, it is important to note those that may play a rôle in the estimate of the normality or the adequacy of the ration. One of them, without doubt, and probably a very important one, is the character and amount of the ration preceding the test ration.

Before steers 1 to 12 arrived at the Experiment Station, November 3, 1918, all but Nos. 6 and 7 had been kept in a barn for a week or ten days; previously they had been on pasture. No. 2 had been kept in a barn about 3 weeks before arriving at the station, and Nos. 6 and 7 were taken off pasture only a day or two before arriving. After arrival they were all given hay, but also had the run of a small pasture back of the barn. Up to November 27 no records were kept of the hay fed, and during this time the steers no doubt got a little grass, but this could not have been an appreciable amount, since the pasture was a very small one for 12 steers and the season was so far advanced that the grass they did get was probably fairly well dried out. On November 27 they were all placed in their stalls and the first records of feed were kept. Steers A and B were received at the station on November 14, 1919, and immediately fed hay only, to approximate the amount they would consume.

Under the circumstances, therefore, it can be seen that not a little difference obtained in the pre-experimental feeding habits of some of these animals. Some had been on pasture, some had been fed hay, but in all probability placing any of the animals upon a ration exclusively of hay resulted in a

material alteration in the general character of the intestinal residue or fill. Hence it is by no means certain that with our steers the rations were necessarily inadequate because the body-weight did not remain at the initial level. A long-continued weight series would be necessary to prove positively the inadequacy of the ration, although we have very strong evidence that the maintenance rations were deficient for practically all the animals. It is, therefore, clear that these losses in weight known to have taken place during the maintenance period might have been ascribable to changes in fill, although there is no positive evidence that the entire loss in body-weight during the maintenance period can be accounted for by change in fill alone.

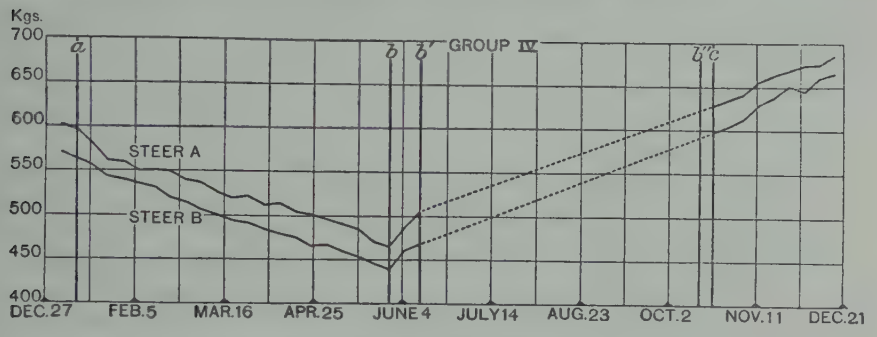


FIG. 22.—Body-weight curves of steers A and B, Group IV.

The vertical line *a* indicates the end of the hay-maintenance period and the beginning of the submaintenance period on hay alone; the vertical line *b* indicates the beginning of the 2-week period of realimentation with hay alone; *b'* indicates the beginning of the pasture period; *b''* indicates the beginning of the short period when the steers were brought back from pasture and fed unknown amounts of hay alone; and *c* indicates the beginning of the fattening period with hay and grain.

It is necessary to examine the further stages in ration alteration for some light on this subject. At the dates of strict ration curtailment with practically all the groups except the control steers (which were not subjected to feed reduction), the curves all show a distinctly rapid loss during the first month or six weeks, with a relatively steady loss thereafter. Curtailing the amount of hay unquestionably reduced the fill considerably, not only the dry matter of fill, but possibly the water of fill,[a] so that it is not unreasonable to ascribe a portion of the seemingly rapid loss in weight at the start to this change in fill, and it is probable that the slope of the curve after the first month following curtailment of ration more nearly represents the true steady loss in body material other than fill. This general conception seems to be reasonably demonstrated by the course of the curve following the ingestion of an increased amount of hay at the end of the submaintenance period, when for one week all the animals were given essentially double the submaintenance

[a] Grouven (loc. cit., pp. 135 and 149) found decreased water in feces, but increased water in fill in animals slaughtered after short periods of fasting One would expect on this basis an increase in the proportion of water in fill, an increase that might offset absolute loss. This finding of decreased water in feces and increased water in fill is not as inconsistent as it might at first sight appear. Vrybürg (Recueil de Médecine Vétérinaire, 1907, 84, p. 510) maintains that text-books on physiology are in error in stating that fluids pass by the rumen, for he has shown experimentally that most of the fluid is found in the rumen and that the water consumed would not necessarily dilute or moisten feces about to be expelled.

ration, i. e., the original maintenance amount. This meant an addition of from 3 to 6 kg. per day to the submaintenance ration, or in the case of 7 days an addition of from 21 to 42 kg. During this week all the submaintenance animals, except steers 1 and 10, showed a gain in weight of considerable magnitude, i. e., from 14 to 25 kg. (See Table 15, p. 99.) Since undoubtedly a major part of this increased hay ration was burned in the body, it is obvious that this increase in hay *per se* can not account for *all* of the increase in weight. But since food such as hay, containing a large amount of crude fiber, is rather slow in passing through the digestive tract, it is probable that this tendency to retention increased the fill, accounting in part for increased body-weight. On the other hand, the increased amount of hay ingested must have resulted in a larger absorption and retention of water in the fill. Hence it is highly probable that an appreciable part of the increase in the hay ingested contributed to the fill both directly and indirectly and that the increase in weight during the first few days may have been in large part due to the increase of fill.

We still have to consider the fact that with 2 steers, Nos. 1 and 10 (as shown in Fig. 20), very slight increases in weight during this period of refeeding with hay were noted, much less than with any of the other animals that had been on submaintenance rations. With No. 10 this is readily explainable. It was at first planned to carry him for an indefinite period following submaintenance on the original maintenance allowance of hay only to see whether he would again acquire his initial weight. For the first few days after May 5 this plan was disturbed, some feed being withheld, as he was used for a prolonged respiration experiment, and the actual daily weights of hay given from May 6 to 12 were therefore much less than the amount intended, the daily average being about 6 kg. (5.6 kg. of water-free substance). There was thus an actual daily increase in his feed for the entire week of only 1.5 kg. of water-free substance per day, on the average, and while the hay records show that an attempt was made to make up the feed he lost as a result of the prolonged respiration experiment, this was not accomplished. During the last week of the submaintenance period, steer 10 drank on the average 13.0 kg. of water per day, while for the next 7 days (with the slight average increase in water-free substance in hay of 1.5 kg. per day) the water consumed averaged 14.0 kg. daily, an increase of but 1 kg. of water daily. Under these conditions the very slight increase in weight from May 6 to 12, shown in Fig. 20, is readily explained.

The situation is somewhat similar with steer 1, inasmuch as a 48-hour respiration experiment (which brought down his weight 13 kg.) was included in the 7-day maintenance period. This animal had an increase in hay amounting to 4.5 kg. (water-free substance) per day. An examination of the records for drinking-water shows that at the close of the period of submaintenance, namely, from April 28 to May 5, for 8 days the average water consumption was 9.0 kg. For the next 7 days, during 5 of which his hay ration was practically doubled, the water consumption averaged 19.0 kg. per day. Consequently with the increase of 4.5 kg. of water-free substance per day in hay and an increase in water consumption of 10 kg. per day, the fact that there was such a slight difference in the body-weight of this animal between these two periods seems explained by the losses suffered during the first 2 days when he

was fasting, as no attempt was made to compensate later for feed withdrawn. The difference in live weight between the two periods, based on the average of the 7 daily weights of each period, was only 8.0 kg.

The foregoing considerations lead to the conclusion that a large proportion of the increase in weight observed in general with all animals during the week of May 6 to 12 was due to change in fill. The data are suggestive of a possible method of roughly approximating this amount of fill, or more particularly of approximating the amount of the total loss in weight during submaintenance ascribable to changes in fill, on the basis of the following assumptions. For one week following the prolonged period of submaintenance the animals were given a full maintenance ration of hay, during which time there was a progressive increase in weight. By subtracting the average weight during the last week of submaintenance from the average weight during the short hay-maintenance period following submaintenance, an approximate estimate of the changes in weight of fill may be made. This method of computation has been carried out in Table 15 for the animals subjected to submaintenance rations. According to this computation the increases in weight, that is, the

TABLE 15.—*Average gain in weight between last week on submaintenance ration and first week on refeeding with hay alone.*

| Group and steer No. | Average weight during— | | Gain in Weight. |
|---|---|---|---|
| | Last week on submaintenance ration. | First week on refeeding with hay. | |
| | *kg.* | *kg.* | *kg.* |
| Group II: | | | |
| Steer 1 | 457 | 465 | 8 |
| 3 | 383 | 397 | 14 |
| 7 | 352 | 375 | 23 |
| 10 | 456 | 460 | 4 |
| 11 | 386 | 411 | 25 |
| Group III: | | | |
| Steer 6 | 340 | 359 | 19 |
| 8 | 343 | 363 | 20 |
| 9 | 453 | 475 | 22 |
| 12 | 292 | 316 | 24 |
| Group IV: | | | |
| Steer A | 465 | 487 | 22 |
| B | 439 | 462 | 23 |

changes in fill, range from 4 kg. with steer 10 to 25 kg. with steer 11. All of the animals show an increase of 14 or more kg., save Nos. 1 and 10, whose small gains, attributable to ration adjustment and a consequent gross irregularity in water consumption, have just been discussed.

The average value for the increase in weight coincidental with the increase in hay ration is 21 kg., the average for all but steers 1 and 10. Thus the evidence indicates an increase in fill of not far from 20 kg. under the peculiar conditions of feeding represented by a comparison of average weight values at the end of submaintenance with average weight values during a week immediately following on refeeding with hay. This value of 20 kg., while far from

representing the total weight of fill (which both Grouven[a] and Moulton[b] show may be around 60 kg.) does nevertheless show the possibility of the large fluctuations in fill that take place with changes in ration involving a single feedstuff, since it represents an *addition* to fill.

Other features of our experiments throw light upon the amount of fill and the quantitative changes coincident with ration alterations, and to this end analyses of the weight changes in two of the steers put on pasture, as well as a study of the total rate of loss in body-weight on submaintenance will be made.

### EFFECT OF PASTURE ON FILL.

In an exhaustive treatment of the discussion of fill, slaughter tests should obviously be made on different animals, having subjected them previously to various curtailments of ration and some of them to various periods upon pasturage, which should be at least roughly standardized. This was impracticable in our series, but observations upon at least two of our animals throw interesting light upon the question of the effect of pasture upon fill. In our group subjected to two reductions in ration (Group III), two of the animals, Nos. 6 and 9, were turned out to pasture after the one week's feeding with hay from May 6 to 12, but they were brought back to the laboratory for frequent weighing. A general index of the rate of regain of body tissue and fill lost as a result of submaintenance ration may be obtained from an estimate of the length of time required for these animals to regain their original weight after refeeding began. These estimates for Groups II and III are given in Tables 10 and 12. (See pp. 91 and 94.) Disregarding for the moment the differences in the initial body-weights and the noticeable differences in the refeeding rations, it can be seen that all but two of the animals regained their original weight only after 71 or more days. Two regained their original weight in 38 and 41 days, respectively. It is certainly more than a coincidence that of all the steers which had previously been subjected to a reduction in ration, the two which regained their original weight in the shortest time were animals which had been put out to pasture.

The obvious explanation is that with the feeding of green grass the body was overloaded with large masses of fill and water, which tended to bring the animal back rapidly to original weight. That the return to original weight was an index of regain of original body composition is of course not to be thought of for a moment. From the common household experience and, indeed, the general economic experience of the stimulating effect of green feed upon the addition of flesh, it is perhaps not surprising that the grass-fed animals showed these great changes in weight, and we must not overlook the fact that from the standpoint of the supply of growth-stimulating factors these animals had a distinct advantage over those fed on hay and concentrates. Our evidence in general, however, would seem to imply that this advantage could not have weighed heavily in the comparison of the several sets of animals.

A second feature of the regain in weight of these two animals (Nos. 6 and 9) which points strongly toward an enormous increase in fill during the first 40

[a] Grouven, loc. cit., pp. 49 and 133.

[b] Trowbridge, Moulton, and Haigh, Univ. Missouri, Agric. Expt. Sta., Bull. 18, 1915, pp. 9 and 10.

days is the fact that the change in weight after initial weight had been regained is relatively slight (see Fig. 21) and their curves for body-weight tend to remain more nearly flat than in the case of steers 8 and 12, which were given fattening rations throughout the entire period. While it is true, therefore, that steers 6 and 9 rapidly regained their original weight on pasturage, the evidence is strong that this regain in weight was in large part fictitious so far as organized body-tissue is concerned. These two animals had regained their initial weight in about 40 days after the end of the long submaintenance period, but they were of course not in condition for slaughter, and it is obvious that no experienced stockman would have failed to recognize that these were soft, grass-fed animals that would yield but a minimum of dressed beef. This rapid resumption of original weight is, however, a striking proof of the tremendous changes in fill that can take place in the adult steer on pasture, following restricted rations.

While no measurements of the actual fill could be made in this test, it is obvious that such measurements would be of great physiological interest, particularly the determination of the total dry matter in fill. It seems not unlikely that the percentage of water might rise to as high as 95 per cent, as reported by Grouven[a] in the fill of some fasting animals.

## RATE OF LOSS IN WEIGHT ON SUBMAINTENANCE RATIONS AS AN INDEX OF AMOUNT OF FILL.

While thus far in this discussion more prolonged influences of changes in ration have been considered, certain of the data are instructive in that an analysis of the daily body-weights immediately following and preceding the marked reductions in ration is worthy of consideration. Thus, on December 22, after the steers were weighed, 9 of them had their ration reduced. The weights on the day following the cut are significant, and the data are given for all these steers in Table 16, including similar data for steers A and B studied the subsequent year, and for steers 6, 8, 9, and 12 at the time of their second cut in ration, February 8. Examining, first, the data for December 22 to 24, we note that all the animals except one (No. 6) show either no change or a very distinct falling off in weight. No. 6 shows a positive gain of 19 kg. Unfortunately, at this stage of the investigation daily records for water consumption were not made. The protocols show that the weights for steer 6 were 438 kg. on December 18, 439 kg. on December 21, and 422 kg. on December 22, i. e., a drop of 17 kg. in weight just prior to the cut in ration. It would appear, then, as if 422 kg. was a minimum point in the normal weight curve of this animal. Indeed, from the beginning of observation on November 23, 1918, until December 22, 422 kg. chances to be the absolute minimum weight. The increase, therefore, of 19 kg. in the case of steer 6 may readily have been due to an excessive water consumption, of which unfortunately no record was available, and this might easily have been more than enough to wipe out the loss in weight which could be expected from a large decrease in the quantity of matter taken into the alimentary tract. Six other animals showed losses ranging from 7 to 29 kg., and 2 others, Nos. 7 and 9, showed no change in their weight at all.

[a] Grouven, loc. cit., p. 135.

This analysis of the immediate influence of reduction in ration on fill is complicated by the fact that during the early maintenance period with a relatively large ration of hay the water consumption was more regular from day to day, while during the submaintenance period many animals frequently refused to drink at all on one day and then consumed relatively large amounts the next. The general picture, however, drawn from the data in Table 16, bears out the conclusion that a sudden decrease in the amount of water-free

TABLE 16.—*Changes in daily body-weights 24 and 48 hours after reductions in ration, Groups II, III, and IV.*

| Group and Steer. | Body-weight in respect to reduction. | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | Before. | | 24 hours after. | | Change in 24 hours. | 48 hours after. | | Change in 48 hours. |
| | Date. | Weight. | Date. | Weight. | | Date. | Weight. | |
| | | *kg.* | | *kg.* | *kg.* | | *kg.* | *kg.* |
| Group II:[1] | | | | | | | | |
| Steer 1... | Dec. 22 | 587 | ..... | ..... | ..... | Dec. 24 | 559 | −28 |
| Steer 3... | | 504 | ..... | ..... | ..... | | 475 | −29 |
| Steer 7... | | 443 | ..... | ..... | ..... | | 443 | ± 0 |
| Steer 10... | | 596 | ..... | ..... | ..... | | 571 | −25 |
| Steer 11... | | 518 | ..... | ..... | ..... | | 505 | −13 |
| Group III:[1] | | | | | | | | |
| Steer 6... | Dec. 22 | 422 | ..... | ..... | ..... | Dec. 24 | 441 | +19 |
| Steer 8... | | 478 | ..... | ..... | ..... | | 471 | − 7 |
| Steer 9... | | 563 | ..... | ..... | ..... | | 563 | ± 0 |
| Steer 12... | | 407 | ..... | ..... | ..... | | 397 | −10 |
| Group III:[2] | | | | | | | | |
| Steer 6... | Feb. 8 | 402 | Feb. 9 | 400 | −2 | Feb. 10 | 392 | −10 |
| Steer 8... | | 408 | | 411 | +3 | | 399 | − 9 |
| Steer 9... | | 531 | | 526 | −5 | | 518 | −13 |
| Steer 12... | | 353 | | 349 | −4 | | 347 | − 6 |
| Group IV:[3] | | | | | | | | |
| Steer A.... | Jan. 10 | 601 | Jan. 11 | 605 | +4 | Jan. 12 | 591 | −10 |
| Steer B.... | | 569 | | 574 | +5 | | 552 | −17 |

[1] With Groups II and III body-weights were obtained on the morning of Dec. 22, before feeding. On this date the first cut in rations was made. No weights were recorded on Dec. 23, so the changes in weight due to the reduction could not be noted until 48 hours later, i. e., on Dec. 24.

[2] With Group III the second cut in rations was made on Feb. 8, after the steers were weighed.

[3] With Group IV body-weights were recorded at 2 p. m., Jan. 10. At $4^{h}45^{m}$ p. m. the first cut in feed was made, and body-weights were recorded thereafter at 2 p. m., Jan. 11, Jan. 12, etc.

substance fed in the form of hay results, on the whole, in a distinct loss in weight of the animal the next day, a fact which in turn suggests strongly that this change in weight is due to a decrease in the total fill, which is both directly and indirectly affected by a reduction in the amount of water-free substance in the hay consumed.

On February 8, when steers 6, 8, 9, and 12 were subjected to a second feed reduction, 3 out of the 4 again showed a loss in weight on the following days, relatively small though it was, and a greater loss on the second day, February 10. Steers A and B had both actually increased slightly in weight 24 hours after the ration was reduced, namely, on January 11, but 48 hours after the reduction both showed a distinct decrease from their original weight. It

is clear that the data given in this table are not to be looked upon as positive proof of the point raised that major variations in live weight over short periods of time are largely the result of variations in weight of fill, but they are certainly suggestive as to further experimental lines. It does not seem impossible that the apportionment of drinking-water offered animals might be so regulated experimentally as to rule out materially the inequalities noted from day to day and thus more clearly define the individual causes of variations in fill.

TABLE 17.—*Changes in daily body-weights during 4 consecutive days after the second reduction in ration, Group III.*

| Steer and date[1] (1919). | Hay (as eaten). | Water. | Body-weight.[2] | Change in weight after reduction.[3] |
|---|---|---|---|---|
| Steer 6: | *kg.* | *kg.* | *kg.* | *kg.* |
| Feb. 7 | 5.3 | 7.0 | 406 | ..... |
| 8 | 3.2 | 18.0 | 402 | ..... |
| 9 | 3.1 | 4.5 | 400 | − 2 |
| 10 | 1.5 | 9.0 | 392 | −10 |
| 11 | 3.2 | 16.0 | 388 | −14 |
| 12 | 4.7 | 9.0 | 387 | −15 |
| Steer 8: | | | | |
| Feb. 7 | 5.4 | 9.0 | 409 | ..... |
| 8 | 3.2 | 13.5 | 408 | ..... |
| 9 | 1.5 | 0.0 | 411 | + 3 |
| 10 | 3.2 | 0.0 | 399 | − 9 |
| 11 | 4.8 | 13.5 | 388 | −20 |
| 12 | 3.2 | 0.0 | 398 | −10 |
| Steer 9: | | | | |
| Feb. 7 | 6.4 | 9.0 | 535 | ..... |
| 8 | 4.3 | 16.0 | 531 | ..... |
| 9 | 2.2 | 7.0 | 526 | − 5 |
| 10 | 4.2 | ..... | 518 | −13 |
| 11 | 6.4 | 13.5 | 509 | −22 |
| 12 | 4.2 | 13.5 | 512 | −19 |
| Steer 12: | | | | |
| Feb. 7 | 4.5 | 9.0 | 354 | ..... |
| 8 | 2.7 | 9.0 | 353 | ..... |
| 9 | 2.7 | 9.0 | 349 | − 4 |
| 10 | 1.3 | 18.0 | 347 | − 6 |
| 11 | 2.4 | 13.5 | 340 | −13 |
| 12 | 4.1 | 0.0 | 335 | −18 |

[1] The barn temperature, Feb. 7 to 12, was approximately 13°, 12°, 12°, 10°, 9°, and 10°C., on the respective dates.

[2] The body-weights were obtained on the morning of the respective dates, before hay or water was consumed.

[3] The second reduction in ration began with the morning feed of Feb. 8.

The data in Table 16 have been confined to the weights obtained 24 and 48 hours after cuts in ration, but we may go a little further and analyze the weights for the 4 and 5 consecutive days following these reductions in ration. This is done in Tables 17 and 18. In Table 17 the weights of Nos. 6, 8, 9, and 12 are given for the first 4 days after the feed reduction, and they show a pronounced progressive daily loss with all 4 animals following this second curtailment in ration, a daily loss which is infinitely greater than the normal

daily loss experienced by these animals over a longer period. (See general slopes of the curves in Fig. 21.) Thus, during the entire period of the second reduction in ration, from February 8 to May 5, the average daily loss per animal is as follows: No. 6, 0.56 kg.; No. 8, 0.76 kg.; No. 9, 0.87 kg.; and No. 12, 0.69 kg. During the first 4 days after feed reduction, on the other hand, the actual loss per day was as follows: No. 6, 3.8 kg.; No. 8, 2.5 kg.; No. 9, 4.8 kg.; and No. 12, 4.5 kg.

TABLE 18.—*Changes in daily body-weights during 5 consecutive days after reduction in ration, Group IV.*

| Steer and date (1920). | Hay (as eaten). | Water. | Body-weight. | Change in weight after reduction. | Remarks. |
|---|---|---|---|---|---|
| Steer A: | *kg.* | *kg.* | *kg.* | *kg.* | The dates represent 24-hour periods beginning and ending at 2 p. m. The body-weights were obtained at the end of the 24-hour periods; the data for hay and water represent the total amount consumed during the 24 hours. The barn temperature on these dates was about 10° C. The reduction in rations began with the 4.45 p. m. feed, Jan. 10. |
| Jan. 9–10 | 9.09 | 27.0 | 601 | ..... | |
| 10 11 | 4.55 | 28.0 | 605 | + 4 | |
| 11 12 | 4.55 | 8.0 | 591 | −10 | |
| 12 13 | 4.55 | 16.5 | 588 | −13 | |
| 13 14 | 4.55 | 11.0 | 583 | −18 | |
| 14 15 | 4.55 | 9.0 | 578 | −23 | |
| Steer B: | | | | | |
| Jan. 9–10 | 9.09 | 46.5 | 569 | ..... | |
| 10 11 | 4.55 | 30.5 | 574 | + 5 | |
| 11 12 | 4.55 | 0.0 | 552 | −17 | |
| 12 13 | 4.55 | 28.0 | 565 | − 4 | |
| 13 14 | 4.55 | 23.0 | 551 | −18 | |
| 14 15 | 4.55 | 26.0 | 562 | − 7 | |

With steers A and B, the data, as shown in Table 18, indicate likewise a very great loss during the first 5 days following the curtailment in ration. The difficulty of securing a true representative average loss in periods as short as 4 or 5 days, where great fluctuations in weight occur from day to day, is obvious.

For example, if the first 4 days after feed reduction are taken as a basis for illustrating losses in live weight due to reduction, both steers A and B show a total loss of 18 kg., but if an additional day is included steer A shows a loss of 23 kg. and steer B a loss of only 7 kg., having increased 11 kg. over his weight on the previous day, due to great irregularity in water consumption and retention of urine. This brings out again the uncertainty in the use of individual daily weights as a basis for argument, considering the great influence on live-weight variations exerted by irregularity in the expulsion of fecal matter and in the consumption of water. However, the figures obtained by dividing the total loss for a few days immediately following ration curtailment by the number of days represented have a greater significance with respect to the influence exerted on live weight by the fill than the values representing the average loss per day throughout the entire submaintenance period, since it is obvious that the large daily average losses during a few days could have included no material loss in tissue, whereas the average daily loss during a long period did involve a material loss in tissue as well as in fill. It is quite clear, therefore, that we have here evidence of a more notice-

able *rate* of loss for the first few days following the cut in ration than we have for the average weight-loss throughout the entire period, and thus we are undoubtedly dealing with a specific effect of the cut in ration *per se*.

### LOSS IN WEIGHT DURING THE FIRST MONTH COMPARED WITH THAT DURING THE LAST MONTH OF A REDUCED RATION.

The comparisons thus far made, save perhaps that involved in a consideration of the effect of pasture upon fill, have for the most part dealt with weights separated by but a few days. As previously emphasized, all weight tests of short duration are complicated greatly by variations in water intake. On the other hand, with a constant curtailed ration and a constant activity, it is reasonable to assume that the drafts upon body material will be reasonably constant from week to week and, indeed, from month to month. How did the weight-loss of these animals during the first month compare with the monthly rate of loss thereafter? We have already shown (Table 11, p. 92) that with Group II somewhat over 50 per cent of the total loss took place during the first month, while the remainder was distributed over a period of 3 months. After the first month the rate of loss averages very closely 19 kg. per month for all the animals. If, therefore, this amount be deducted from the average loss of these animals during the first month, a quantitative suggestion of the variation taking place in the amount of fill following ration reduction may be legitimately secured. During the first month of curtailed ration the animals in Group II lost amounts varying from 55 kg. with steer 7 to 72 kg. with steer 11. A strict comparison between Groups II and III is not permissible, as the ration curtailment of Group III was managed somewhat differently from that of Group II, and the two groups must therefore be treated independently. The average value representing loss in weight for Group II is 64 kg. during the first month, representing both fill and tissue. If we subtract from this the average loss per month (which is 19 kg.)[a] for the 3 subsequent months (when the fill could not have changed materially and the loss must largely represent tissue and its normally accompanying water),[b] the balance, 45 kg., represents *change* in fill, fill representing not merely dry matter, but the semi-liquid mass or ballast in the intestinal tract. It is important to realize that this 45 kg. is by no means the whole of the fill, but it may be taken as the change in fill. While in this discussion only two explanations for weight changes are admitted, namely, change in weight of fill and change in weight of organized body flesh or tissue, the possible changes in body-fluids such as blood-volume and lymph must not be entirely overlooked. Although they are admittedly not considered in this treatment, we believe they probably are not of sufficient magnitude to affect seriously our general conclusion.

If, as is subsequently demonstrated (see p. 172), we can use circumference measurements taken at the chest just back of the elbow as an index of the

[a] The use of this figure as an index of the probable loss of tissue during the first month is open to the objection that the metabolism measurements show that there was a much higher metabolism during the first month and that the loss of actual body-tissue would in all probability be somewhat greater than 19 kg. In lieu of the impossibility of estimating this loss more closely, however, we have simply used this figure as a rough approximation.

[b] Water fluctuations must be in large part in fill, as Moulton (Journ. Biol. Chem., 1920, **43**, p. 67) has shown that undernutrition does not alter the percentage of water in fat-free flesh.

deposition of tissue, unaffected by fill, a further confirmation of this approximate figure of 45 kg. as the probable change in fill undergone by these submaintenance animals is had. Thus, if we consider the circumference measurements, as recorded in Table 45 (p. 174), we will note that the chest circumference after the beginning of refeeding remains reasonably constant with all the animals until about June 10. From there on the measurements indicate clearly an increase in chest circumference, which we interpret as meaning an actual, true deposition of fat or flesh. While no material changes in the circumferences occur from May 6 up to this date, the increases in body-weight are very large, in many instances being considerably more than 50 kg. and on the whole not far from 45 to 50 kg. Since this represents the first stage of refeeding from submaintenance, the addition of tissue must have been very small, indicating again largely a change in fill.

The animals in Group II show a singular uniformity of agreement in the estimate of this change in fill. When we consider the animals in Group III, the situation is not dissimilar, although quantitatively on a somewhat different basis. (See Table 13, p. 95). During the first month the loss on the average was 43 kg., considerably less than that noted with Group II, since the feed reduction was also less. During the period from March 3 to April 16, after which the animals apparently ceased to lose weight, the loss averaged, as a matter of fact, no more than with Group II, namely, 19 kg. per month, although they had been on an even more drastic feed-level for over 2 months. Assuming that this represented, however, the regular loss of tissue and accompanying water, and subtracting this from the average loss during the first month, we find 24 kg. as an index of the change in fill occurring with these animals. We have not carried the analysis further and attempted to note the possible change in fill during the second cut in ration with these animals.

The picture presented with Group III is nearly duplicated with steers A and B (see Table 14, p. 96). The average loss per month during the last 3⅔ months for the 2 animals was 25 kg. During the first month the loss in weight was 47 kg. with steer A and but 30 kg. with steer B. Deducting the 25 kg. representing presumably the regular loss due to tissue and its normal accompanying water, we find that with steer A the amount representing the change in fill is 22 kg., while with steer B it is but 5 kg. As has been repeatedly emphasized, however, these two animals were given altogether different treatment from the other steers, and (a fact bearing more particularly upon this immediate question) all the evidence indicates that these animals were already on a distinctly submaintenance ration before any large curtailment in ration was made.

### REPORTED WEIGHTS OF FILL.

In the discussion thus far reference has frequently been made, in more or less quantitative terms, to additions to or withdrawals from fill, on the assumption that rather large changes in fill can be induced in the course of a relatively short time. Data with regard to the amount of fill in animals is singularly lacking, when one considers the millions of animals that have been slaughtered for consumption and, indeed, the large number of animals that have been subjected to slaughter tests. As indicative of some of the most careful work, we may cite that of Trowbridge, Moulton, and Haigh,[a] from whose data

[a] Trowbridge, Moulton, and Haigh, Univ. Missouri, Agric. Expt. Sta., Bull. 18, 1915, pp. 9 and 10.

the actual weight of fill for a number of mature steers may be computed. These authors have clearly recognized the importance of disregarding, in metabolism and other measurements that have reference to nutrition, the gross body-weight as such, arguing properly that the warm empty weight, that is, weight without fill, is alone of physiological significance, and they have carefully computed the percentage of empty to live weight. The great differences in fill that may be found in animals of the same weight are shown strikingly in two of their animals. With their steer No. 596, which had a live weight of 560 kg., the fill amounted to 35 kg., and with their steer No. 590, which was only 3 months older and weighed but 6 kg. more, the fill was 83 kg. or more than twice that of the other steer. It is unfortunate, however, that the exact previous treatment of these animals prior to slaughter, especially the length of time between the last feed and the moment of slaughter, is not clearly indicated in the special bulletins[a] referred to.

TABLE 19.—*Average weight of fill in steers (Haecker).*

| Continuous stall feeding. | | | Steers from pasture. | | |
|---|---|---|---|---|---|
| No. of steers. | Live weight. | Weight of fill. | No. of steers. | Live weight. | Weight of fill. |
| | *kg.* | *kg.* | | *kg.* | *kg.* |
| 3 | 272 | 51.3 | 2 | 272 | 56.2 |
| 4 | 318 | 54.0 | 2 | 318 | 54.9 |
| 3 | 363 | 54.9 | 1 | 363 | 66.7 |
| 3 | 408 | 59.0 | 1 | 454 | 85.7 |
| 4 | 454 | 57.2 | 1 | 544 | 74.8 |
| 3 | 499 | 59.4 | ..... | ..... | ..... |
| 3 | 544 | 51.7 | ..... | ..... | ..... |
| 2 | 590 | 68.5 | ..... | ..... | ..... |
| 1 | 635 | 79.8 | ..... | ..... | ..... |
| 1 | 680 | 70.3 | ..... | ..... | ..... |

Haecker[b] reports the average of a considerable number of observations on normal steers, giving the average weight of fill, which he designates as "waste" or "contents of digestive tract." His data, which we have converted from pounds to kilograms, represent the average values for steers, including both stall-fed and pasture-fed animals.

For those animals approximating the weights of our animals the data are given in Table 19. Haecker concludes that in animals above 700 pounds (318 kg.) the weight of fill is measurably greater with the pasture-fed steers than with those that were stall-fed.

Grouven,[c] whose historical contributions have challenged our attention so frequently, records certain data of value in this connection. Thus, in 1862, he weighed the fill of a steer having a live weight of 408 kg., and found it to be 63 kg. Another steer, weighing 387 kg., had 61 kg. of fill. Both these values,

[a] Trowbridge, Moulton, and Haigh, Univ. Missouri, Agric. Expt. Sta., Bull. 18, 1915; *ibid.*, Bull. 30, 1919, p. 65.

[b] Haecker, Univ. Minnesota, Agric. Expt. Sta., Bull. 193, 1920, Tables XXIII and XXV, pp. 42 and 43.

[c] Grouven, loc. cit., pp. 133 and 135.

obtained under ordinary conditions of feeding, are quite in line with those found by Haecker. The fill averaged 85 per cent of water. A 420-kg. steer, slaughtered after fasting 5 days, had 41 kg. of fill, and another steer, weighing 523 kg., slaughtered at the end of 8 days of fasting, still had 70 kg. of fill. In both these instances with fasting steers the fill averaged 95 per cent of water. This is an amount strikingly at variance with the percentage of water in feces noted by us with our steers. Thus, according to our own experience (see p. 127), the water-content of feces becomes somewhat less with reduced rations, and it is decidedly less when the steer is fasting than when he is on a maintenance ration.

All of these data, both early and modern, prove that from 10 to 20 per cent of the gross live weight of a well-fed steer may be in the form of inert, unorganized material in the intestinal tract.

### SCIENTIFIC AND ECONOMIC IMPORTANCE OF DETERMINING THE INFLUENCE OF FILL UPON BODY-WEIGHT CHANGES.

From the foregoing analysis it is clear that relatively large variations in fill accompany alterations in ration. This is, to be sure, more clearly shown with the animals in Group II than with either those in Group III or Group IV, but the picture is the same in all cases, except that it is somewhat less accentuated in the last two groups. From this evidence it seems clear that in all experiments with ruminants where an alteration in ration is made, special care must be taken to account for the disturbing influence of changes in fill upon body-weight. Individual body-weights recorded under conditions of change in ration, even with uniform water consumption, we believe have little, if any, value. Just how long a period should be over which the weight should be taken before assuming that figures are truly representative of a change in weight of body-tissue, is still a matter of much debate. Professor Armsby, as far back as 1898,[a] advocated averaging 10 days' weights together. Thus, if an experiment was to begin on the first of the month and continue for several months, he would record the average weight from the first to the tenth day, inclusive, then from the second to the eleventh, the third to the twelfth, etc. By this means he succeeded in wiping out gross fluctuations and obtained a weight curve which he believed was more truly typical of the actual changes in tissue. Even this procedure, although extremely clever and unquestionably giving a truer picture than any other method in use at that time, still leaves the two ends of the experiment, often the most critical and important features of it, unprotected. The character and amount of the preceding ration must be known and, indeed, quantitatively. A knowledge of the amounts of drinking-water and, if possible, feces and urine, is also important in interpreting the significance of weight changes.

In the experimental laboratory no factor may be left unmeasured. Our own belief is strongly in favor of continuous collection of data, permitting the computation on each day of the insensible perspiration. Indeed, it is most unfortunate that practically all of the earlier work (including that done in American as well as in Continental laboratories) although giving data for changes in body-weights, weights of urine and feces, and feed, do not permit

[a] Armsby, Pennsylvania State College, Agric. Expt. Sta., Bull. 42, 1898, p. 30.

of the accurate computations of the insensible perspiration, owing to the lack of information as regards the time relations between the weights. With an animal standing quietly in a stall, on uniform feed, the insensible perspiration should remain reasonably constant from day to day. Changes in feed affect this profoundly. Our own investigations now in progress give most important evidence on this point. But pending the adoption of technique for measurement of the insensible perspiration in experimental laboratories, one may certainly expect that the various workers in animal nutrition may adopt some uniform standard for weighing, and particularly some uniformity in the time of weighing relative to the time of feeding and watering, which will render each experimental series more intelligible and more comparable. This is especially to be emphasized in experimental series where animals are weighed only at the beginning and end of a very protracted feeding period.

The paucity of knowledge with regard to the character and amount of the contents in the digestive tract of ruminants, the pronounced effect that this ballast undoubtedly exerts upon changes in weight, and the fact that live weight is the basis for sale of meat animals both before and after fattening makes it seem imperative that scientists should no longer neglect in their slaughter tests the factor of fill or be content with the simple statement as to the actual weight of fill. It is of the utmost importance that not only the weight of fill, but also the percentage composition, at least the water-content, should be known. It is quite probable that there are variations in the composition of the fill in different parts of the digestive tract, and these should also be determined. The contributions already made from the Missouri station by Moulton and his collaborators[a] should be much further extended and supplemented by more elaborate chemical analyses. Body measurements, particularly circumferences, should be taken with the special view of throwing light upon changes in girth at paunch, which may reasonably be expected to indicate more nearly changes in fill than actual deposition of flesh. Too little has already been done upon this question. The admirable method in the Missouri studies of referring measurements to warm empty weight, thus ruling out the weight of fill, is strongly to be commended. Until, however, sufficient evidence is accumulated to make the data on warm empty weight of actual value in the sale of slaughtered animals, it is obligatory that a study of fill accompany such tests. It is quite clear that when feed is given but 2 hours before slaughter, in one instance, and in another instance feed has been withheld for 12 or 24 hours, the amount of fill will be subject to considerable variations.

Finally, the economic importance of a standardized degree of uniformity in the method of weighing animals prior to sale stands out clearly as a result of the foregoing analysis. Information kindly furnished us by Professor Moulton states that it is now the practice at the Missouri Experiment Station to allow a fast of from 12 to 24 hours between the last feed and the time of slaughter. This is based upon the fact that the packers in the West follow a somewhat similar procedure, since they are of the opinion that the animal

[a] Trowbridge, Moulton, and Haigh, Univ. Missouri, Agric. Expt. Sta., Bull. 18, 1915.

bleeds, dresses, and handles better. In the case of our own animals (the steers of Groups II and III, which were slaughtered at Brighton, Massachusetts), there seems to have been no regular routine. At Brighton, animals that arrive in the morning are not fed if slaughtered that day and if sold on the date of arrival. If they are kept over, they are fed, but they are just as likely to be sold before feeding as after feeding. Our own 9 steers were at Brighton over 24 hours, and they had not been fed before slaughtering. This was, however, an exception, in that they were sold on the basis of dressed weight, while live stock is ordinarily sold on the hoof.

The former experience of one of us (E. G. R.) on a farm in Iowa shipping cattle to the Chicago market will likewise indicate a situation not uncommon. Shipments were made so that live stock arrived in Chicago early in the morning. It was the custom, in that section of the state, to change the ration on the evening of the day before shipping and the morning of the day of shipment from corn, which had a very laxative effect, to oats, which acted as a binder, to offset this condition during shipping. The animals were loaded in the cars about 3 p. m. and they received no feed or water, therefore, on that afternoon, so that they would not scour en route and thereby lose weight. After arrival in Chicago, the animals might be fed as much corn as their owners wished before being weighed in. All stock arriving on a certain morning was usually sold before noon of that day.

Animals shipped long distances by railroad probably lose a disproportionate amount of fill, especially if they are shipped off pasture or range, or if they have previously been fed on heavy grain rations, as their feces are noticeably loose. The attempt mentioned above to substitute oats for corn is in the line of correcting losses from this source. Farmers in eastern Iowa, for example, estimate shrinkage in weight of cattle shipped from there to Chicago, a distance of 150 miles, to be 3 per cent of the live weight, although the cattle are on the cars only from 12 to 15 hours and also are shipped during the night, when it is cool. In a standardized market like Chicago, the question of fill is by no means disregarded, as the seller has an option between weighing cattle in the condition in which they arrive or watering them and giving them all the shelled corn they will eat before being weighed, accepting in this latter case a 3 per cent shrinkage or deduction in the weight.

From these considerations, therefore, it is clear that the amount and chemical composition of fill and its distribution in the intestinal tract is a matter that should receive immediate attention, since the results should find great economic application in helping establish more standard conditions, not only for the beginning and end of scientific tests in animal nutrition, but likewise for the sale and market of different animals. It would appear as if the complete withdrawal of food for a definite length of time might more nearly equalize comparable conditions for an estimate of the proportion of fill to total weight. But here again undoubtedly great differences in fill will be found when the rations vary in character. The importance, wherever possible, of basing measurements upon weight less fill is most strongly to be commended to animal physiologists. That the best method for doing this has in all probability not yet been found does not lessen in the slightest the obligation of physiologists to recognize this fundamental point.

## General Conclusions with Regard to Body-weight as Affected by Ration Curtailment.

Entirely aside from all transitory, sudden weight fluctuations due to changes in water consumption and readjustment of intestinal ballast or fill, the several curves show a persistent, prolonged decrease in weight coincidental with ration curtailment, which would naturally be expected. Deficient food must of necessity mean draft upon body-substance, and this draft was in all cases, save with the controls, very considerable in amount. Of the four weight charts, that for the controls shows the anomalous condition which unfortunately exists, that for a period of nearly 2 months this group lost weight on a supposedly maintenance feed. The weight lost, while not perhaps excessive, nevertheless was sufficiently marked to lead to the conclusion that the ration was not a maintenance ration. Practically all the other animals, as shown in all the other charts, likewise lost weight during the so-called maintenance period, although this period was usually very short. All this tends to confirm our belief that practically every animal in the entire series began the ration curtailment not on a maintenance ration, but on a ration somewhat lower than maintenance. Employing the best accepted standards for the dry matter in feed required per 1,000 pounds of weight, we made every effort to predict a maintenance ration for these animals at the start, but contrary to most other workers, instead of having to decrease our so-called maintenance ration, we would have had to increase it, had we made any adjustment to secure maintenance level based on gross live weight.

Following the striking curtailment in ration with Group II, the general slope of the curve for each steer shows a pronounced falling off in the weight, rather rapid at first, and then slowly persisting, but with evidence of constancy in weight at the lower base-level during the last two weeks. With all the steers in Group III, which underwent the two curtailments in ration, we find that the plateau or level occurs usually not far from the first of April, indicating that the second ration adjustment brought the animals practically into balance so far as the body-weight is concerned.

With Group IV, the steady, downward trend of the curves, even during the very last few weeks, shows more strikingly than was shown with any of the other groups the fact that the ration was far from sufficient to maintain these animals even at this lowered weight-level and lowered metabolic level. With these 2 animals the loss in body-weight per day at the end of the submaintenance period was still very considerable. There was (as is seen in Table 14, p. 96), an average loss of 25 kg. per month during the last 3⅔ months. This corresponds to a loss of approximately 0.8 kg. per day, and this loss can be taken as representing real tissue and water accompanying tissue, which must necessarily be restored to the organism during the refeeding period. This loss of 0.8 kg. per day, even at the end of the submaintenance period, is larger than with any of the other groups. Thus, with Group II the loss per month for the last 3 months was 19 kg. on the average (as shown in Table 11, p. 92), corresponding to approximately 0.6 kg. per day. With Group III the loss during the last 1½ months, i. e., from March 3 to April 16, also averaged, with rather wide deviations to be sure, 19 kg., or 0.6 kg. per day. It must be recalled, however, that with this group a plateau was reached approximately on April 16 and that if the average total loss had been divided by 2 months

instead of 1½ months, this would have lowered somewhat the loss per month. All the evidence, however, is perfectly clear that with animals A and B the loss per month was greater than with any of the other groups and is probably to be explained in large part by the fact that the curtailment in ration (which amounted to about 60 per cent) was made upon a supposedly maintenance ration which was in reality deficient for maintenance.

On refeeding the loss in fill was easily made up. One has but to recall the rapidity in gain of body-weight of the animals put upon pasture, Nos. 6 and 9. But on the basis of a loss of 0.8 kg. per day it would be utterly impossible to get the flesh and fat back onto the animal frame so quickly. In other words, the post-pasture fill must have been larger than the maintenance fill, i. e., the fill at the start, in order to make up for all the fill lost and in addition for the weight of the tissue lost so rapidly.

The findings, therefore, on this series of weight charts are what one could predict, namely, with submaintenance rations rapid loss in weight, with a tendency, however, for the weight with certain groups to become constant when the live weight has reached a level on which the quantity of feed suffices to maintain it. This tendency is unquestionably accelerated by the fact that (as will be demonstrated in a subsequent section) the standard metabolism is noticeably lowered as a result of the undernutrition.

## DRINKING-WATER.

Not until about two months after the beginning of the first year's work, i. e., on February 6, 1919, was it feasible to secure daily records of drinking-water. By this time Groups II and III were well along in their curtailed ration period. Due to the paucity of assistants and the difficulty of working in an unheated barn, the only method available during the first year for determining the amount of water taken was to keep a record of the number of pailfuls consumed by the animal and make ocular estimates to the nearest quarter pailful. As each pail held approximately 20 pounds and the estimates to one-fourth pailful could be readily made, in the final tabulation of figures we have felt safe in giving 7-day averages on the basis of even half kilograms. The water given steers 1 to 12 usually was at the extremely low temperature of 2.5° C. With steers A and B during the year 1919–20 an entirely different procedure was followed in that the animal was weighed just before and just after watering and the individual weights of water are known in all probability to half a kilogram. The averages for the 2-week periods are certainly known well within half a kilogram.

### Average Daily Water Consumption.

The data for the water consumption of Groups I, II, and III, expressed as average values per day for 7-day periods, are given in Table 20. It is to be recalled that from May 6 to 12 all these animals were upon a supposedly maintenance hay ration, and that after May 12 fattening rations were usually given. Prior to May 6 all animals were on curtailed rations except Nos. 2, 4, and 5, which were retained as controls. The animals, however, were not all of the same weight, and obviously those subjected to curtailed rations fell off noticeably in weight. But for purposes of general inspection we may consider the total daily water consumption, irrespective of size of animal, as given in Table 20.

The consumption on the normal or maintenance ration may be roughly taken as that shown by Nos. 2, 4, and 5 up to May 13. Of these animals we find that No. 5 drank on the whole somewhat larger amounts per day than the other two steers, No. 2 drinking the smallest amounts, a proportionality

TABLE 20.—*Average daily water consumption, steers 1 to 12.*[1]

| Date. | Group I. | | | Group II. | | | | | Group III. | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Steer 2. | Steer 4. | Steer 5. | Steer 1. | Steer 3. | Steer 7. | Steer 10. | Steer 11. | Steer 6. | Steer 8. | Steer 9. | Steer 12. |
| 1919 | kg. | kg. | kg. | kg. | kg. | kg. | kg. | kg. | kg. | kg. | kg. | kg. |
| Feb. 6 to Feb. 9.. | 14.0 | 12.0 | 16.0 | 5.5 | 12.0 | 6.0 | 9.0 | 8.0 | 13.0 | 8.0 | 12.5 | 9.0 |
| Feb. 10 Feb. 16.. | 9.5 | 18.0 | 17.0 | 6.0 | 12.0 | 8.5 | 7.0 | 9.0 | 9.5 | 5.0 | 9.0 | 8.0 |
| Feb. 17 Feb. 23.. | 12.5 | 14.5 | 16.0 | 8.0 | 10.5 | 6.5 | 9.0 | 7.5 | 8.0 | 5.0 | 7.0 | 7.0 |
| Feb. 24 Mar. 2.. | 13.5 | 16.5 | 20.0 | 9.0 | 10.5 | 6.5 | 8.0 | 10.0 | 8.5 | 8.0 | 10.5 | 8.5 |
| Mar. 3 Mar. 9.. | 12.0 | 15.0 | 16.5 | 7.5 | 11.5 | 6.0 | 7.0 | 6.0 | 5.5 | 5.5 | 8.5 | 4.0 |
| Mar. 10 Mar. 16.. | 7.0 | 15.5 | 20.0 | 9.5 | 10.0 | 2.5 | 9.0 | 7.0 | 9.0 | 7.0 | 6.0 | 6.0 |
| Mar. 17 Mar. 23.. | 8.5 | 15.0 | 19.5 | 8.0 | 11.5 | 5.5 | 6.0 | 7.0 | 7.0 | 5.5 | 4.0 | 6.0 |
| Mar. 24 Mar. 30.. | 9.5 | 13.5 | 20.0 | 5.0 | 11.5 | 2.5 | 4.0 | 7.0 | 8.5 | 4.5 | 5.0 | 2.5 |
| Mar. 31 Apr. 6.. | 18.5 | 17.0 | 19.0 | 10.5 | 12.0 | 10.5 | 10.5 | 10.0 | 9.0 | 8.0 | 12.0 | 8.0 |
| Apr. 7 Apr. 13.. | 19.5 | 19.0 | 20.5 | 10.5 | 14.0 | 10.5 | 12.0 | 9.5 | 12.5 | 9.0 | 11.0 | 7.0 |
| Apr. 14 Apr. 20.. | 15.0 | 19.0 | 24.0 | 10.5 | 12.5 | 8.5 | 11.0 | 10.0 | 14.5 | 8.5 | 8.0 | 6.5 |
| Apr. 21 Apr. 27.. | 18.0 | 18.0 | 23.0 | 10.5 | 12.0 | 9.5 | 11.5 | 10.5 | 13.0 | 10.5 | 12.5 | 7.0 |
| Apr. 28 May 5.. | 16.5 | 16.5 | 23.0 | 9.0 | 12.0 | 8.0 | 13.0 | 12.0 | 13.5 | 10.0 | 11.0 | 7.5 |
| May 6 May 12.. | 16.0 | 15.0 | 26.0 | 19.0 | 18.0 | 14.0 | 14.0 | 18.5 | 15.5 | 14.0 | 17.5 | 15.5 |
| May 13 May 19.. | 21.0 | 26.0 | 29.0 | 24.5 | 30.0 | 20.5 | 24.5 | 23.0 | ..... | 19.0 | ..... | 18.5 |
| May 20 May 26.. | ..... | 27.5 | 33.0 | 20.5 | 25.5 | 21.0 | 19.5 | 25.5 | ..... | 28.0 | ..... | 23.5 |
| May 27 June 2.. | ..... | 28.0 | 29.0 | 21.5 | 30.0 | 19.5 | 26.5 | 28.5 | ..... | 30.5 | ..... | 26.0 |
| June 3 June 9.. | ..... | 26.0 | 25.5 | 23.5 | 26.0 | 19.5 | 23.0 | 26.0 | ..... | 30.0 | ..... | 20.5 |
| June 10 June 16.. | ..... | 31.5 | 30.5 | 24.0 | 28.0 | 17.5 | 18.0 | 22.0 | ..... | 37.0 | ..... | 27.0 |
| June 17 June 23.. | ..... | 34.5 | 34.5 | 22.5 | 31.5 | 17.0 | 20.5 | 25.0 | ..... | 33.5 | ..... | 17.5 |
| June 24 June 30.. | ..... | 39.0 | 36.0 | 27.0 | 44.5 | 24.5 | 21.5 | 32.5 | ..... | 42.0 | ..... | 31.5 |
| July 1 July 7.. | ..... | 38.5 | 46.0 | 40.0 | 51.5 | 25.5 | 28.5 | 34.0 | ..... | 52.0 | ..... | 38.5 |
| July 8 July 14.. | ..... | 46.5 | 38.5 | 34.5 | 42.5 | 32.0 | 25.5 | 33.5 | ..... | 44.5 | ..... | 31.5 |
| July 15 July 21.. | ..... | 50.5 | 43.0 | 41.0 | 53.5 | 33.5 | 42.5 | 33.5 | ..... | 51.0 | ..... | 37.5 |
| July 22 July 28.. | ..... | 52.0 | 48.5 | 42.0 | 57.0 | 36.0 | 42.5 | 41.5 | ..... | 54.5 | ..... | 36.5 |
| July 29 Aug. 4.. | ..... | 48.5 | 44.5 | 39.5 | 51.0 | 33.0 | 44.5 | 39.0 | ..... | 49.5 | ..... | 40.0 |
| Aug. 5 Aug. 11.. | ..... | 50.0 | 41.0 | 42.5 | 54.5 | 31.0 | 46.0 | 39.0 | ..... | 53.0 | ..... | 37.5 |
| Aug. 12 Aug. 18.. | ..... | 49.0 | 45.5 | 40.5 | 49.0 | 30.0 | 53.5 | 36.5 | ..... | 52.0 | ..... | 36.5 |
| Aug. 19 Aug. 25.. | ..... | 53.5 | 44.0 | 39.5 | 49.5 | 31.0 | 58.5 | 39.0 | ..... | 46.5 | ..... | 39.5 |
| Aug. 26 Sept. 1.. | ..... | [2]36.5 | [2]39.5 | 31.0 | 42.5 | 26.0 | 37.0 | 34.0 | ..... | 46.0 | ..... | 39.0 |
| Sept. 2 Sept. 8.. | ..... | ..... | ..... | 30.0 | 43.5 | 23.5 | 49.5 | 33.5 | ..... | 45.5 | ..... | 36.5 |
| Sept. 9 Sept. 15.. | ..... | ..... | ..... | 29.5 | 34.0 | 22.5 | 31.5 | 25.5 | ..... | 37.0 | ..... | 24.0 |
| Sept. 16 Sept. 22.. | ..... | ..... | ..... | 32.5 | 41.0 | 25.5 | 41.0 | 31.0 | ..... | 42.5 | ..... | 31.0 |
| Sept. 23 Sept. 29.. | ..... | ..... | ..... | 30.0 | 42.0 | 24.5 | 39.0 | 29.0 | ..... | 41.5 | ..... | 30.5 |
| Sept. 30 Oct. 6.. | ..... | ..... | ..... | 32.5 | 44.0 | 24.5 | 44.5 | 30.0 | ..... | 41.0 | ..... | 33.5 |
| Oct. 7 Oct. 13.. | ..... | ..... | ..... | 38.5 | 47.5 | 29.0 | 45.5 | 32.5 | ..... | 46.5 | ..... | 37.0 |
| Oct. 14 Oct. 20.. | ..... | ..... | ..... | 32.5 | 34.0 | 24.0 | 38.0 | 26.5 | ..... | 32.5 | ..... | 28.5 |
| Oct. 21 Oct. 27.. | ..... | ..... | ..... | 30.0 | 40.0 | 23.5 | 41.0 | 27.0 | ..... | 30.5 | ..... | 30.0 |
| Oct. 28 Nov. 3.. | ..... | ..... | ..... | 14.5 | 32.5 | 20.0 | 37.0 | 32.5 | ..... | 34.0 | ..... | 30.5 |

[1] The average body-weights for these steers between Feb. 3 and May 5 were as follows: No. 2, 442 kg.; No. 4, 494 kg.; No. 5, 587 kg.; No. 1, 478 kg.; No. 3, 403 kg.; No. 7, 367 kg.; No. 10, 476 kg.; No. 11, 407 kg.; No. 6, 360 kg.; No. 8, 363 kg.; No. 9, 481 kg.; No. 12, 312 kg.

[2] Represents the average daily water consumption from Aug. 26 to 28 only.

that is not strikingly different from that representing the actual average weights of the animals. Thus, during the period under consideration, namely, from February 6 to May 12, inclusive, steer 2 weighed on the average about 440 kg., steer 4 about 500 kg., and steer 5 about 590 kg. Certain striking differences, however, in the daily amounts consumed from week to week are noted, particularly with steer 2 in the 3 weeks from March 10 to March

30, when noticeably less water was consumed than at any other time. Decreases in the amounts consumed by the other animals during this period are not to be observed, and no simple explanation is at hand. According to the normal data secured with Group I, therefore, approximately speaking, a 500-kg. steer, receiving not far from 8 kg. of dry matter in the form of hay per day, drank about 18 kg. of water per day.

For Groups II and III, which were on curtailed rations after December 22, no normal values, i. e., prior to ration curtailment, are available, and hence for comparison with normal data we must refer directly to the values for Nos. 2, 4, and 5. From such a comparison one instantly sees that in all cases the amounts of water consumed by Groups II and III were noticeably less than those by the control group. The main deduction, therefore, from this inspection of the tabular matter, is that with the curtailment of feed there was a pronounced reduction in the amount of water consumed, a reduction which was reasonably uniform for all of the nine animals which were given curtailed rations.

No data with regard to the urine or feces of animals 1 to 12 are at hand. We can not, therefore, determine with these steers how the water consumption influenced those factors which make for loss of water from the body, i. e., the water lost in urine, feces, and insensible perspiration. From an analysis, however, of the data for steers A and B in Figs. 17 and 18 (pp. 86 and 87), in which a comparison of the daily weights of water, urine, feces, and feed is made, it is quite clear that the influence of water consumption upon the water lost in urine and feces was not great, for with the widest variations in water consumption the loss in urine and feces remained practically unaltered.

### Relationship between Water-free Substance in Feed and Water Consumed on Maintenance and Submaintenance Rations.

The amount of drinking-water taken by an animal is commonly assumed to be dependent to a large extent upon the water-free substance in feed consumed, the idea being that the water supplements the original dry matter in the green grass, which has been dried out in the curing of the hay, so that the bulk of the ration is largely fluid and easily passed into the various sections of the complicated digestive tract of the ruminant. In his book, which may be taken as an index of the best teaching in Europe certainly, Kellner[a] states that for each kilogram of dry matter in feed oxen take from 4 to 5 kg. of water, with a higher environmental temperature calling for a larger water intake. He emphasizes the amount of heat required to warm the large masses of cold water commonly consumed by large ruminants and, assuming that this heat is extra heat over and above the regular heat-production, he shows that the ingestion of large amounts of digestible feed is essential to furnish the calories thus employed, i. e., approximately 10 per cent of the total heat requirement for the day. The matter has special significance in our studies, since the water given to steers 1 to 12 had an average temperature of 2.5° C. for the greater part of the period of submaintenance feeding. Undoubtedly Kellner's recommendation to take the chill off the water offered animals, in order to conserve heat, is worthy of special consideration in connection with feeding and metabolism tests. In our own work it is perhaps particularly unfortunate

[a] Kellner, Die Ernährung der landwirtschaftlichen Nutztiere, 9th ed., Berlin, 1920, p. 185.

that we did not recognize this important factor at the start, for Kellner especially emphasizes the draft made upon the heat-production of undernourished animals as a result of their having to warm up the cold water.

TABLE 21.—*Average daily water consumption per kilogram of water-free substance in feed, steers 1 to 12.*

| Date. | Group I. | | | Group II. | | | | | Group III. | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Steer 2. | Steer 4. | Steer 5. | Steer 1. | Steer 3. | Steer 7. | Steer 10. | Steer 11. | Steer 6. | Steer 8. | Steer 9. | Steer 12. |
| 1919 | kg. | kg. | kg. | kg. | kg. | kg. | kg. | kg. | kg. | kg. | kg. | kg. |
| Feb. 6 to Feb. 9 | 2.2 | 1.7 | 2.0 | 1.3 | 3.2 | 1.9 | 2.2 | 2.4 | 3.4 | 2.1 | 2.6 | 2.7 |
| Feb. 10 Feb. 16 | 1.5 | 2.5 | 2.1 | 1.5 | 3.2 | 2.6 | 1.7 | 2.7 | 3.4 | 1.7 | 2.4 | 3.3 |
| Feb. 17 Feb. 23 | 1.9 | 2.0 | 2.0 | 2.0 | 2.8 | 2.0 | 2.2 | 2.3 | 2.8 | 1.7 | 1.8 | 2.8 |
| Feb. 24 Mar. 2 | 2.0 | 2.3 | 2.5 | 2.2 | 2.8 | 2.0 | 2.0 | 3.0 | 3.0 | 2.8 | 2.8 | 3.4 |
| Mar. 3 Mar. 9 | 1.8 | 2.0 | 2.0 | 1.8 | 3.1 | 1.8 | 1.7 | 1.8 | 1.9 | 1.9 | 2.2 | 1.7 |
| Mar. 10 Mar. 16 | 1.0 | 2.1 | 2.4 | 2.3 | 2.7 | 0.8 | 2.2 | 2.1 | 3.2 | 2.4 | 1.6 | 2.4 |
| Mar. 17 Mar. 23 | 1.2 | 1.9 | 2.3 | 2.0 | 3.1 | 1.7 | 1.5 | 2.1 | 2.5 | 1.9 | 1.1 | 2.4 |
| Mar. 24 Mar. 30 | 1.4 | 1.8 | 2.4 | 1.2 | 3.1 | 0.8 | 1.0 | 2.1 | 3.0 | 1.6 | 1.3 | 1.0 |
| Mar. 31 Apr. 6 | 2.7 | 2.2 | 2.2 | 2.6 | 3.2 | 3.2 | 2.6 | 3.0 | 3.1 | 2.8 | 3.2 | 3.2 |
| Apr. 7 Apr. 13 | 2.8 | 2.6 | 2.4 | 2.6 | 3.8 | 3.2 | 2.9 | 2.9 | 4.5 | 3.1 | 2.9 | 2.8 |
| Apr. 14 Apr. 20 | 2.2 | 2.5 | 2.8 | 2.6 | 3.4 | 2.6 | 2.7 | 3.1 | 5.2 | 2.9 | 2.2 | 2.7 |
| Apr. 21 Apr. 27 | 2.6 | 2.4 | 2.7 | 2.7 | 3.2 | 2.9 | 2.8 | 3.2 | 4.5 | 3.6 | 3.3 | 2.9 |
| Apr. 28 May 5 | 2.5 | 2.2 | 2.7 | 2.6 | 3.2 | 2.4 | 3.2 | 3.6 | 4.8 | 3.4 | 2.9 | 3.1 |
| May 6 May 12 | 2.0 | 2.1 | 2.5 | 2.4 | 2.0 | 2.3 | 2.5 | 2.8 | 2.4 | 2.2 | 2.2 | 2.5 |
| May 13 May 19 | 3.6 | 2.7 | 2.8 | 2.4 | 3.4 | 2.7 | 3.6 | 2.6 | ..... | 2.3 | ..... | 2.5 |
| May 20 May 26 | ..... | 2.9 | 3.0 | 2.0 | 3.2 | 2.3 | 2.6 | 2.6 | ..... | 2.9 | ..... | 2.9 |
| May 27 June 2 | ..... | 2.8 | 2.6 | 2.4 | 2.9 | 2.5 | 3.5 | 3.3 | ..... | 3.4 | ..... | 3.2 |
| June 3 June 9 | ..... | 2.5 | 2.2 | 2.4 | 2.7 | 2.2 | 3.1 | 2.5 | ..... | 2.9 | ..... | 2.3 |
| June 10 June 16 | ..... | 2.8 | 2.5 | 2.4 | 2.3 | 2.2 | 2.4 | 2.2 | ..... | 2.9 | ..... | 2.6 |
| June 17 June 23 | ..... | 2.7 | 2.5 | 2.4 | 2.6 | 2.3 | 3.0 | 2.6 | ..... | 3.1 | ..... | 2.0 |
| June 24 June 30 | ..... | 3.3 | 2.5 | 2.4 | 3.2 | 2.5 | 2.8 | 2.6 | ..... | 3.4 | ..... | 3.1 |
| July 1 July 7 | ..... | 3.2 | 3.3 | 2.9 | 3.5 | 2.6 | 3.5 | 2.7 | ..... | 3.9 | ..... | 4.0 |
| July 8 July 14 | ..... | 3.4 | 2.6 | 2.7 | 3.1 | 2.7 | 1.8 | 3.6 | ..... | 3.7 | ..... | 3.1 |
| July 15 July 21 | ..... | 3.4 | 2.8 | 2.7 | 3.3 | 2.6 | 3.4 | 2.5 | ..... | 3.5 | ..... | 3.5 |
| July 22 July 28 | ..... | 3.4 | 3.1 | 2.7 | 3.5 | 2.7 | 3.6 | 3.1 | ..... | 3.8 | ..... | 3.3 |
| July 29 Aug. 4 | ..... | 3.2 | 2.8 | 2.6 | 3.1 | 2.3 | 3.0 | 2.6 | ..... | 3.4 | ..... | 3.4 |
| Aug. 5 Aug. 11 | ..... | 3.4 | 2.7 | 2.8 | 3.5 | 2.4 | 2.9 | 2.8 | ..... | 3.8 | ..... | 3.2 |
| Aug. 12 Aug. 18 | ..... | 3.0 | 2.8 | 2.7 | 3.0 | 2.2 | 3.2 | 2.5 | ..... | 3.4 | ..... | 2.8 |
| Aug. 19 Aug. 25 | ..... | 3.3 | 2.7 | 2.5 | 3.0 | 2.3 | 3.5 | 2.7 | ..... | 3.0 | ..... | 3.1 |
| Aug. 26 Sept. 1 | ..... | [1]3.0 | [1]3.2 | 2.0 | 2.7 | 1.9 | 2.3 | 3.0 | ..... | 3.1 | ..... | 3.0 |
| Sept. 2 Sept. 8 | ..... | ..... | ..... | 2.7 | 3.2 | 2.0 | 3.2 | 2.5 | ..... | 3.5 | ..... | 2.9 |
| Sept. 9 Sept. 15 | ..... | ..... | ..... | 2.2 | 2.2 | 2.0 | 2.1 | 2.0 | ..... | 2.7 | ..... | 2.4 |
| Sept. 16 Sept. 22 | ..... | ..... | ..... | 2.4 | 2.5 | 1.9 | 2.4 | 2.3 | ..... | 3.1 | ..... | 2.4 |
| Sept. 23 Sept. 29 | ..... | ..... | ..... | 2.1 | 2.6 | 2.2 | 2.3 | 2.3 | ..... | 3.1 | ..... | 3.2 |
| Sept. 30 Oct. 6 | ..... | ..... | ..... | 2.2 | 2.8 | 1.9 | 2.4 | 2.3 | ..... | 2.9 | ..... | 2.7 |
| Oct. 7 Oct. 13 | ..... | ..... | ..... | 2.5 | 3.0 | 2.2 | 2.5 | 2.4 | ..... | 3.4 | ..... | 3.0 |
| Oct. 14 Oct. 20 | ..... | ..... | ..... | 2.4 | 2.5 | 2.1 | 2.4 | 2.5 | ..... | 3.7 | ..... | 2.9 |
| Oct. 21 Oct. 27 | ..... | ..... | ..... | 2.1 | 2.6 | 2.3 | 2.6 | 2.5 | ..... | 2.8 | ..... | 2.8 |
| Oct. 28 Nov. 3 | ..... | ..... | ..... | 2.1 | 2.8 | 2.0 | 2.1 | 2.7 | ..... | 2.7 | ..... | 2.6 |

[1] For Aug. 26 to 28 only.

Knowing for all of our animals the weight of water-free substance in the feed, which was primarily hay, we can easily compute the average daily water consumption per kilogram of water-free substance in feed. (See Tables 21 and 22.) Of the 14 animals for which this ration was determined, Nos. 2, 4, and 5 were fed a maintenance amount of hay alone up to May 13, and hence are our control animals. Steers A and B were fed hay for maintenance for 14 days, i. e., from December 27, 1919, to January 10, 1920. In considering the water consumed per kilogram of water-free substance in hay, we must bear

in mind that the irregularities in total daily water consumption, which are in part to be explained by differences in body-weights, are here more or less equalized by the basis of computation, because the hay fed was in every instance computed on the basis of body-weight.

For steers 2, 4, and 5, prior to May 13, 1919, the average daily water consumption per kilogram of water-free substance in feed ranges from a low value of 1.0 kg. with steer 2 to a high value of 2.8 kg. with steers 2 and 5. On the other hand, there is a rather remarkable uniformity, the values averaging for steers 4 and 5 not far from 2.5 kg. and for steer 2 somewhat less. These ratios are measurably less than the commonly accepted value of 4 kg. Examining the rather meager normal data for steers A and B in Table 22, we

TABLE 22.—*Average water consumption per day and per kilogram of water-free substance in feed per day, steers A and B.*

| Period. | Date. | Steer A. | | Steer B. | |
|---|---|---|---|---|---|
| | | Per day. | Per kg. water-free substance in feed per day. | Per day. | Per kg. water-free substance in feed per day. |
| | 1919–1920 | *kg.* | *kg.* | *kg.* | *kg.* |
| 1 | Dec. 27 to Jan. 10 | 26.0 | 3.8 | 24.5 | 3.8 |
| 2 | Jan. 10 Jan. 24 | 12.5 | 3.1 | 15.0 | 3.7 |
| 3 | Jan. 24 Feb. 7 | 12.5 | 3.0 | 11.0 | 2.7 |
| 4 | Feb. 7 Feb. 21 | 12.5 | 3.0 | 13.0 | 3.2 |
| 5 | Feb. 21 Mar. 6 | 12.5 | 3.3 | 14.5 | 3.8 |
| 6 | Mar. 6 Mar. 20 | 11.0 | 2.8 | 12.5 | 3.2 |
| 7 | Mar. 20 Apr. 3 | 14.0 | 3.9 | 15.0 | 4.2 |
| 8 | Apr. 3 Apr. 17 | 11.0 | 3.2 | 12.0 | 3.3 |
| 9 | Apr. 17 May 1 | 13.5 | 3.7 | 13.0 | 3.6 |
| 10 | May 1 May 15 | 12.5 | 3.5 | 14.0 | 3.9 |
| 11 | May 15 May 29 | 15.0 | 4.2 | 11.0 | 3.0 |
| 12 | May 29 June 12 | 22.0 | 2.8 | 21.5 | 2.7 |
| 13 | Oct. 22 Nov. 5 | 29.5 | 2.7 | 32.5 | 3.0 |
| 14 | Nov. 5 Nov. 19 | 36.0 | 2.6 | 43.5 | 3.2 |
| 15 | Nov. 19 Dec. 3 | 37.0 | 3.0 | 49.0 | 3.6 |
| 16 | Dec. 3 Dec. 17 | 33.0 | 2.5 | 48.5 | 3.6 |

find that during the period of maintenance the two values are alike, i. e., 3.8 kg. for each animal, and are very close to the commonly accepted normal of 4 kg. Since the conditions under which steers 1 to 12 were studied were noticeably different from the conditions under which A and B were studied, it is necessary for us to lay greater weight upon the normal values found with steers 2, 4, and 5, namely, a rough figure of 2.5 kg., rather than the higher value of 3.8 kg. found with steers A and B. Reference to this point will be made later.

On the curtailed rations the quantity of water consumed per kilogram of water-free substance in feed is considerably altered. With steer 3 it remains persistently above 2.7 kg. With steer 7 it is low until March 31 and thereafter fairly high. The same may be said with regard to steer 10 and, to a certain

extent, with steer 11. Steer 1 shows low values for February 6 to March 30 and subsequently a nearly constant value of 2.6 kg. With the group of steers which were given two reductions in ration even more irregularity is noted, for the quantities range from a minimum of 1.9 kg. to a maximum of 5.2 kg. with steer 6, from 1.6 kg. to 3.6 kg. with steer 8, from 1.1 kg. to 3.3 kg. with steer 9, and from 1.0 kg. to 3.4 kg. with steer 12. It is to be seen, however, that practically all of the values, even the maximum values, lie below the conventional value of 4 kg.

With steers A and B an entirely different picture is presented, and in the interpretation of the results emphasis must again be laid upon the fact that steers A and B were studied in an entirely different building under different conditions, were confined to metabolism stalls the entire time, did not have any daily exercise, and (as is seen from an examination of the temperatures in Table 23, p. 118) were subjected for the most part to somewhat *lower* environmental temperatures than were steers 1 to 12. On the other hand, it is to be remembered that the feed curtailment did not begin until January 10 with steers A and B, while it began on December 22 with steers 1 to 12, a little over 2 weeks earlier. Consequently, the progress of the undernutrition with steers A and B may be stated to be generally about 2 weeks later in the calendar year than in the case of the other 12 animals, and hence the temperature for February 14 to 21 in 1919, which was on the average 13.5° C., represents the average environmental temperature to which these animals were exposed in a stage of undernutrition which approximately corresponds to that occupied by steers A and B during the week of March 1 to 8, 1920, during which time the actual temperature was about 11° C. In Table 23 (see p. 118), therefore, the temperatures are more or less directly comparable on the same line, and while it is seen that there are not very great differences in temperature, almost invariably the temperatures in the dairy barn were somewhat lower than those in the sheep barn. Probably what is of still greater importance, however, is the fact that steers A and B had a much more regular life, with no exercise, and were given more frequent attention on the part of the assistants, so that one can draw comparisons between the results on steers A and B and the other 12 steers only with a considerable degree of reserve. The water consumption did, however, drop off very noticeably with the curtailment of feed, as with the first year's steers. The water to dry-matter ratios are high during the first 14 days, i. e., prior to ration curtailment, in fact, they nearly approximate Kellner's value of 4.0 kg. Thereafter, during the feed cuts, the ratios for these animals remain on the whole slightly higher than the average for the first year's groups. But it is important to note that one animal in the first group, namely, steer 3, gave ratios essentially as high as those noted with steer B.

Close examination of these ratios shows that they underwent with rather remarkable uniformity a fundamental change after March 31. That is, all the animals subjected to submaintenance rations, except No. 3, showed rather low values up to March 31 and considerably higher values thereafter. This is likewise true with control animal No. 2 and, to a certain extent, with control animals Nos. 4 and 5, but it is by no means so strikingly exhibited. To explain this marked difference in the relationship between the water intake and feed at this time is very difficult. In general, the rations ingested

remained essentially the same throughout the entire period from February 6 to May 5, with practically all animals. Certainly no striking alteration in the feed ingested was made around March 31.

### INFLUENCE OF ENVIRONMENTAL TEMPERATURE ON WATER CONSUMPTION.

It was at first thought that some alterations in barn temperature might have accounted for this change. To determine this point we have given in Table 23 the average barn temperatures, as obtained from a recording thermometer. Emphasis is here laid upon the fact that for the first year's work the records were made in the sheep barn and for the second year's work, i. e., with steers A and B, in an entirely different building, the dairy barn. As is to be expected, the temperatures gradually rise as the spring approaches, but there seemingly is nothing exhibited in the temperature records to explain the rather pronounced change in the water to dry-matter ratio pointed out above.

TABLE 23.—*Average barn temperature per week.*

| Sheep barn. | | Dairy barn. | | Sheep barn. | | Dairy barn. | |
|---|---|---|---|---|---|---|---|
| Date. | Temp. | Date. | Temp. | Date. | Temp. | Date. | Temp. |
| 1918–19 | °C. | 1920 | °C. | 1919 | °C. | 1920 | °C. |
| Dec. 13 to 20..... | 20.5 | Jan. 3 to 10..... | 9.0 | Mar. 7 to 14..... | 17.0 | Mar. 22 to 29..... | 17.0 |
| Dec. 20 27..... | 17.0 | Jan. 10 12..... | 10.0 | Mar. 14 21..... | 17.0 | Mar. 29 Apr. 5.. | 16.0 |
| Dec. 27 Jan. 3... | 12.0 | Jan. 12 19..... | 6.0 | Mar. 21 28..... | 20.0 | Apr. 5 12..... | 15.5 |
| Jan. 3 10..... | 10.0 | Jan. 19 26..... | 8.0 | Mar. 28 Apr. 4... | 15.0 | Apr. 12 19..... | 18.0 |
| Jan. 10 17..... | 10.5 | Jan. 26 Feb. 2... | 6.0 | Apr. 4 11..... | 19.0 | Apr. 19 26..... | 17.5 |
| Jan. 17 24..... | 15.0 | Feb. 2 9..... | 12.5 | Apr. 11 18..... | 20.0 | Apr. 26 May 3.. | 18.5 |
| Jan. 24 31..... | 14.0 | Feb. 9 16..... | 13.5 | Apr. 18 25..... | 20.0 | May 3 10..... | 19.0 |
| Jan. 31 Feb. 7... | 12.5 | Feb. 16 23..... | 11.0 | Apr. 25 May 2.. | 28.0 | May 10 17..... | 19.0 |
| Feb. 7 14..... | 11.5 | Feb. 23 Mar. 1.. | 9.0 | May 2 9..... | 24.0 | | |
| Feb. 14 21..... | 13.5 | Mar. 1 8..... | 11.0 | May 9 16..... | 23.0 | | |
| Feb. 21 28 ..... | 15.0 | Mar. 8 15..... | 14.0 | May 16 23..... | 24.5 | | |
| Feb. 28 Mar. 7... | 18.0 | Mar. 15 22..... | 13.0 | | | | |

A further analysis of the influence of environmental temperature upon amount of drinking-water consumed may be made. The question arises as to whether, with essentially the same feed-intake, the average consumption of drinking-water will vary from week to week with considerable changes in barn temperature. To study this point, we have drawn off in Table 24 the average daily water consumption for steers 1 to 12 in two consecutive weekly periods at two different times. In one instance there was a difference of 5° C. in environmental temperature and in the other instance 8° C. During the week March 21 to 27 the average barn temperature was 20° C.; the next week it was 15° C. It will be seen that even with essentially constant feed conditions the consumption of drinking-water was measurably greater with practically all the animals during the second week, i. e., with the colder weather, and, indeed, this increase in water consumption is coincidental with the change in the ratio of water to dry matter in feed, cited in Tables 21 and 22.

Somewhat later, April 18 to 24, the average temperature of the barn was 20° C., and the following week 28° C. Here the water consumption during the first week, that is, the colder week, was in 7 cases slightly greater, in 1

case the same, and in 4 cases slightly less than during the second or warmer week. While numerically the greater number of cases show uniformity with the findings during the 2 weeks from March 21 to April 3, inclusive, most of the animals show practically no change in this second test. This is in striking contrast to the first test, where the increases during the colder weather were very pronounced. Practically, the picture in the second test is one showing little, if any, effect of temperature on water consumption, and hence it would appear as if external temperature at or about the temperatures we employed was without regular effect upon the water consumption.

TABLE 24.—*Average daily water consumption at different environmental temperatures, steers 1 to 12.*

| Group and steer No. | Mar. 21–27 20.0°C. | Mar. 28–Apr. 3. 15.0°C. | Change with colder temperature. | Apr. 18–24 20.0°C. | Apr. 25–May 1. 28.0°C. | Change with colder temperature. |
|---|---|---|---|---|---|---|
| Group I: | *kg.* | *kg.* | *kg.* | *kg.* | *kg.* | *kg.* |
| Steer 2.... | 5.0 | 16.5 | +11.5 | 19.0 | 15.0 | +4.0 |
| Steer 4.... | 13.0 | 15.0 | + 2.0 | 18.5 | 16.5 | +2.0 |
| Steer 5.... | 19.0 | 22.5 | + 3.5 | 23.5 | 22.0 | +1.5 |
| Group II: | | | | | | |
| Steer 1.... | 5.0 | 12.0 | + 7.0 | 9.5 | 11.5 | −2.0 |
| Steer 3.... | 12.5 | 13.5 | + 1.0 | 12.5 | 12.0 | +0.5 |
| Steer 7.... | 2.0 | 8.0 | + 6.0 | 9.5 | 9.0 | +0.5 |
| Steer 10.... | 4.0 | 10.5 | + 6.5 | 13.0 | 11.0 | +2.0 |
| Steer 11.... | 6.0 | 9.5 | + 3.5 | 11.5 | 10.5 | +1.0 |
| Group III: | | | | | | |
| Steer 6.... | 7.0 | 9.0 | + 2.0 | 13.5 | 15.0 | −1.5 |
| Steer 8.... | 3.0 | 8.5 | + 5.5 | 9.0 | 9.5 | −0.5 |
| Steer 9.... | 1.5 | 11.5 | +10.0 | 10.5 | 11.5 | −1.0 |
| Steer 12.... | 3.5 | 7.0 | + 3.5 | 7.0 | 7.0 | ±0.0 |

Although steers A and B were measured under very different conditions, to test this particular point of the possible influence of environmental temperature upon the water consumption, having hay ingestion essentially constant, we also give a comparison with these animals in two periods where the average temperature varied from 4° to 6.5° C. The results are given in Table 25. During the last week in January the barn temperature was actually 6.5° C. lower than during the first week in February, and the water consumption with both animals increased during the second week. Similarly, from March 15 to 22 to the following week there was an increase in the average temperature of 4° C. and here we find likewise an actual increase in water consumption with the higher temperature. Steers A and B, therefore, give results indicating a greater daily water consumption when the barn temperature is higher. It still remains a fact, however, that the noticeable change in the water to dry-matter ratio, noted about March 30 with steers 1 to 12, is coincidental with an average fall in barn temperature of about 5° C., accompanied by a distinct increase in water consumption on the part of all 12 animals. In lieu of further explanation it would appear as if the fall of 5° C. in average barn temperature resulted in an increase in water consumption which was reflected in the higher water to dry-matter ratios, although this evidence is contradicted by the observation on steers A and B.

TABLE 25.—*Average daily water consumption at different environmental temperatures, steers A and B.*

| Steer. | Jan. 26 to Feb. 2. 6.0°C. | Feb. 2 to 9. 12.5°C. | Change with higher temperature. | Mar. 15 to 22. 13.0°C. | Mar. 22 to 29. 17.0°C. | Change with higher temperature. |
|---|---|---|---|---|---|---|
| | *kg.* | *kg.* | *kg.* | *kg.* | *kg.* | *kg.* |
| A | 9.5 | 12.0 | +2.5 | 12.5 | 13.0 | +0.5 |
| B | 8.5 | 15.0 | +6.5 | 11.5 | 15.5 | +4.0 |

## RELATIONSHIP BETWEEN WATER-FREE SUBSTANCE IN FEED AND WATER CONSUMED WITH RESUMPTION OF MAINTENANCE HAY RATION.

During the week of May 6 to 12 the control animals were kept upon a very regular ration, but the 9 other animals, which had been undergoing curtailed rations, were all given an increase in hay only, supposedly sufficient to put them on a maintenance ration for this time. During this week the ratio of water to dry matter remained singularly constant with all these 9 animals, ranging only from 2.0 to 2.8 kg. Indeed, in only one other period during hay feeding, i. e., March 31 to April 6, is the water to dry-matter ratio exhibited by these 9 animals as uniform as during this particular week. It is not unlikely that the accumulation of fill may have induced this uniformity in water consumption. During the period from May 29 to June 12 steers A and B were again given an increased amount of hay to correspond to their supposedly maintenance ration. The values for the water consumed by the two animals per kilogram of water-free substance in feed during this time, namely, 2.8 kg. and 2.7 kg., respectively, show an agreement even better than that noted with the 9 steers of Groups II and III. When one considers the noticeable irregularities in the ratios seen with steers A and B, and in certain instances with the other steers, this uniformity in all animals on the increased hay ration after the submaintenance period is of special significance. Undoubtedly a certain portion of this hay is retained as fill. Since the water consumed would have to equal four times the weight of hay eaten to bring the hay eaten to the consistency of green grass, one would expect that the ratio of drinking-water to hay would actually be somewhat larger during this period, for if a certain portion of the dry hay becomes impregnated with water and is retained as fill, then for every kilogram thus retained there would be approximately 4 kg. of water, thus giving a ratio of 1:4. The fact that the ratio is as low as 1 : 2.4 on the average for all 11 animals suggests a further study of this problem.

It is obvious that there must be a rather intimate relationship between the water to dry-matter ratios, on the one hand, and the change in fill, on the other, particularly in the water-content of fill. As pointed out in a previous section, there is a great paucity of information with regard to the composition, even the moisture-content, of fill, but judging from the results reported by Grouven[a] on the fill of fasting animals and those with a roughage ration, it seems clear that the moisture-content of the fill during fasting actually increases, in striking contrast to the fact that the water-content of the feces

[a] Grouven, loc. cit., pp. 133, 135, and 149.

passed by these animals decreases as the fast progresses. In our own animals it would appear as if during periods of undernutrition the fill becomes richer in water. With these steers, the increased need for extra water to moisten the hay in the fill, upon return to an increased hay ration, may have been such as actually to have withdrawn water from the previously existing excessively water-rich fill, and thus this would account in part, at least, for the low water to dry-matter ratio. In so far, therefore, as this evidence may be used, it would point toward a confirmation of Grouven's contention that the fill of undernourished animals has a high water-content, and one can therefore infer that the addition of dry matter to the ration may actually abstract water from the fill.

### Relationship between Water-free Substance in Feed and Water Consumed on Fattening Rations.

Although the major interest in this report has to deal with the physiology of the animals on submaintenance rations, our data permit the computation of the water to dry-matter ratios for most of our steers during the fattening period. These ratios are given in the lower part of Tables 21 and 22. After May 12, steer 2 was almost immediately turned out to pasture, and hence for this animal no data are available. Steers 4 and 5 show a tendency to a somewhat larger water consumption per kilogram of water-free substance in feed on the fattening rations, the average being 3.1 kg. with steer 4 and 2.8 kg. with steer 5. Group II shows after May 6 ratios quite in line with those exhibited before. In other words, the fattening rations did not materially alter the water to dry-matter ratios, the general picture indicating a water consumption of 2.5 kg. or below for all 5 animals. In this connection it is worthy of note that steer 3, which exhibits a consistently high ratio throughout the entire submaintenance period, maintains essentially the same ratio until August 25, but thereafter the ratio tends to be somewhat lower. Of Group III, 2 were on pasture, i. e., Nos. 6 and 9, and hence no data for them are available. Of the other 2, No. 12 shows ratios quite like those of Group II, while No. 8 shows ratios in general slightly higher. The two animals, A and B, were out on pasture, and hence there are no data for them from June 12 to October 22, after which dates the ratios for both are not unlike those noted in the hay periods, being, if anything, somewhat lower. The average is 2.7 kg. with steer A and 3.4 kg. with steer B, the higher ratio with steer B being possibly accounted for by the higher protein ration fed to this animal. For all of these data it is quite clear that the value commonly accepted of 4 to 5 kg. of water per kilogram of water-free substance in hay is high rather than low, at least with the conditions under which these experiments were carried on.

## FECES.

The fact that most of these animals were subjected to a very drastic curtailment in ration would lead to the supposition that gross alterations in the quantity and nature of the feces might be expected; hence, special attention was given to any possible changes in the regularity of defecation, the physical appearance of the feces, and in the case of steers A and B to their chemical composition. Indeed, all of these factors should be noted at the different nutritive planes and transition periods through which all of these animals passed. It is obvious that, had there been any abnormalities in the appear-

ance of the feces prior to ration curtailment, the animals would not have been retained in the groups for study. There was approximately one month of maintenance feeding on hay with steers 1 to 12 and there were two weeks or more with steers A and B. No quantitative measurements of the amounts of feces nor chemical analyses were made with steers 1 to 12, but in the case of steers A and B a definite part of the program for experimentation was to make such special study of the feces. Inasmuch as steers A and B were placed in suitable metabolism stalls, the collection of feces became a matter of routine, and consequently we have a record of their daily weights of feces throughout practically the entire experimental period, except for the time when they were on pasture.

One of the fundamental precepts in conducting a digestion experiment is that there should be a preliminary feeding period with the feed held constant, to secure equilibrium between income and outgo, the prime object of this being of course to have the feces adjust themselves to the feed given. Unfortunately, with steers A and B we have no normal maintenance periods free from criticism, for our first feces collection with these animals, from December 27 to January 10, representing supposed maintenance, was begun immediately following a cut of about 4.0 kg. in the case of steer A and 3.3 kg. in the case of steer B. During the preliminary period, i. e., prior to December 27, these animals were, therefore, not upon the same ration fed during the first period of feces collection. As Table 1, page 24, will show, the amounts of hay actually eaten by these two animals during the preliminary period was on a daily decreasing scale for a number of days just prior to December 27, when the weighing of feces was begun. It is quite clear, therefore, that in accordance with all previous experimental experience the feces collected between December 27 and January 10 would be in part those representing a somewhat heavier ration than that actually given during this period of collection.

### Regularity of Defecation.

With the express purpose, however, of comparing the regularity of defecation on different nutritive planes, we give in Table 26 the weights of feces for steers A and B during 5 periods, i. e., periods 1, 2, 3, 11, and 16.

In period 1, when supposedly a maintenance ration was given, we find large variations in the feces excretion with both animals. It is important to observe, however, that periodically both animals were placed inside a respiration chamber, which necessitated the withholding of feed for one day. Thus, the low value for feces excretion on January 8–9 with steer A may be accounted for by the fact that on January 7-8 only one-half the normal amount of feed was given, and on January 6–7 no feed was given the animal. Likewise, on the first day of feces collection, December 27–28, when one of the lowest values for feces excretion was observed with steer A, the amount of feed given on the day preceding was approximately only one-half of the regular daily allotment. Similarly, with steer B the feed was not uniform, thus accounting in part at least for the irregularities in defecation, which are strikingly at variance with the regularity in defecation reported by Kühn, Kellner, and others[a] with animals given 10 kg. of hay per day.

[a] Kühn, Kellner, et al., Landw. Versuchsstat., 1894, 44, pp. 15 et seq.

TABLE 26.—*Daily excretion of fresh feces with maintenance, submaintenance, and fattening rations, steers A and B.*

| Period[1] and date. | Feces excreted per day. | | Period[1] and date. | Feces excreted per day. | |
|---|---|---|---|---|---|
| | Steer A. | Steer B. | | Steer A. | Steer B. |
| 1919–20 | | | 1920 | | |
| Period 1: | *kg.* | *kg.* | Period 3—Continued. | *kg.* | *kg.* |
| Dec. 27 to 28..... | 17.14 | 14.72 | Feb. 1 to 2..... | 10.25 | 9.04 |
| Dec. 28 29..... | 19.10 | 17.65 | Feb. 2 3..... | 8.58 | 8.31 |
| Dec. 29 30..... | 20.10 | (2) | Feb. 3 4..... | 3.42 | 3.09 |
| Dec. 30 31..... | 19.24 | 15.33 | Feb. 4 5..... | 7.62 | 8.33 |
| Dec. 31 Jan. 1.. | 21.40 | 19.90 | Feb. 5 6..... | 11.61 | 9.87 |
| Jan. 1 2..... | 23.22 | 20.39 | Feb. 6 7..... | 13.87 | 9.20 |
| Jan. 2 3..... | 19.77 | 18.30 | | | |
| Jan. 3 4..... | 20.38 | 18.96 | Average..... | 8.61 | 8.37 |
| Jan. 4 5... | 20.81 | 19.65 | | | |
| Jan. 5 6..... | 23.94 | 21.65 | Period 11: | | |
| Jan. 6 7..... | 20.01 | 19.48 | May 15 to 16..... | 5.83 | 8.14 |
| Jan. 7 8..... | (2) | 7.73 | May 16 17..... | 8.28 | 7.76 |
| Jan. 8 9..... | 8.31 | 6.40 | May 17 18..... | 6.30 | 6.95 |
| Jan. 9 10..... | 15.89 | (2) | May 18 19..... | 4.98 | 5.90 |
| | | | May 19 20..... | 7.47 | 9.52 |
| Average..... | 19.18 | 16.68 | May 20 21..... | 6.86 | 5.55 |
| | | | May 21 22..... | 6.75 | 8.58 |
| Period 2: | | | May 22 23..... | 7.85 | 7.48 |
| Jan. 10 to 11..... | 21.09 | 15.78 | May 23 24..... | 6.43 | 6.28 |
| Jan. 11 12..... | 15.49 | 13.44 | May 24 25..... | 6.92 | 3.74 |
| Jan. 12 13..... | 13.63 | 11.38 | May 25 26..... | 4.14 | 7.80 |
| Jan. 13 14..... | 9.29 | 8.29 | May 26 27..... | 7.19 | 8.26 |
| Jan. 14 15..... | 10.72 | 9.07 | May 27 28..... | 7.38 | 7.50 |
| Jan. 15 16..... | 7.85 | 8.83 | May 28 29..... | 7.75 | 9.72 |
| Jan. 16 17..... | 9.54 | 10.78 | | | |
| Jan. 17 18..... | 8.63 | 8.57 | Average..... | 6.72 | 7.37 |
| Jan. 18 19..... | 8.14 | 6.96 | | | |
| Jan. 19 20..... | 5.69 | 6.51 | Period 16: | | |
| Jan. 20 21..... | 7.04 | 6.00 | Dec. 3 to 4..... | 14.69 | 28.60 |
| Jan. 21 22..... | 8.47 | 11.53 | Dec. 4 5..... | 15.46 | 26.90 |
| Jan. 22 23..... | 12.27 | 7.74 | Dec. 5 6..... | 23.47 | 27.42 |
| Jan. 23 24..... | 10.38 | 10.11 | Dec. 6 7..... | 24.41 | 23.30 |
| | | | Dec. 7 8..... | 24.39 | 24.17 |
| Average..... | 10.59 | 9.64 | Dec. 8 9..... | 24.94 | 26.76 |
| | | | Dec. 9 10..... | 25.10 | 22.60 |
| Period 3: | | | Dec. 10 11..... | 25.06 | 24.80 |
| Jan. 24 to 25..... | 7.08 | 8.38 | Dec. 11 12..... | 26.03 | 26.76 |
| Jan. 25 26..... | 10.03 | 9.34 | Dec. 12 13..... | 25.26 | 23.60 |
| Jan. 26 27..... | 9.32 | 8.78 | Dec. 13 14..... | 25.59 | 26.20 |
| Jan. 27 28..... | 8.15 | 9.77 | Dec. 14 15..... | 24.28 | 26.44 |
| Jan. 28 29..... | 7.54 | 7.76 | Dec. 15 16..... | 24.59 | 25.24 |
| Jan. 29 30..... | 8.17 | 8.12 | Dec. 16 17..... | 24.58 | 24.14 |
| Jan. 30 31..... | 6.25 | 7.97 | | | |
| Jan. 31 Feb. 1.. | (3) | 9.22 | Average..... | 23.42 | 25.50 |

[1] Period 1 was during the maintenance ration; periods 2, 3, and 11 were during the submaintenance ration, period 11 being the last period with this ration; period 16 was the fourth and last period with fattening rations.

[2] Spilled. [3] Urine and feces accidentally mixed.

As has been repeatedly pointed out by workers in animal nutrition, it is utterly impossible with ruminants to employ the usual method of separation of feces employed with men and dogs, namely, the addition of some coloring matter to the food. With ruminants the experimental period must simply be lengthened to such an extent as to wipe out, in so far as possible, the gross irregularities in unequal defecation. Unfortunately, our data for these steers on a maintenance ration of hay alone give little ground for specific final deductions on the regularity or irregularity of defecation with constant ration. Other investigators, notably Armsby and his associates, have much data on this point which indicate reasonable regularity in the amount of fresh feces passed each day with uniform feed.

With steer A, the feces collection was lost for one day during the first period, but the average excretion of fresh feces for the 13 days in which collection was made amounted to 19.18 kg. per day. Since the curtailment in ration took place at the beginning of the second period, on January 10, this period represents, strictly speaking, a transition in feed-level with a cut of about 50 per cent, during which time the feces were not on a stable quantitative basis representative of the feed-level, and it is not until we get to the third period that we can assume that the average value for feces excretion, 8.61 kg. per day, is characteristic of the low ration. In comparison with these two average figures (19.18 kg. on maintenance and 8.61 kg. on submaintenance), we can see that in period 2 there was obviously a large excretion of feces on January 10–11, 11–12, and 12–13, which more properly belonged to the feed of the previous days. If we accept 8.61 kg. as the normal excretion on a low ration, then the first 3 days of the transition in period 2 contain an excess of approximately 24 kg. of feces properly chargeable to feed of the preceding period. With steer B the ration of 9,090 grams of hay during period 1 produced on the average a somewhat smaller quantity of feces than was the case with steer A, the average value for 12 of the first 14 days being 16.68 kg. of fresh feces per day. Since there was a reduction in feed from 9,090 grams to 4,545 grams of hay per day between periods 1 and 2, the latter must be looked upon as a transition period, and the third period should be accepted as more nearly indicative of the true measure of the feces corresponding to the standard ration, as was done with steer A. In the third period the average weight of feces for 14 days was 8.37 kg. per day. Considering, therefore, 16.68 kg. as the probable feces excretion on the full maintenance ration and 8.37 kg. as that on the low ration, we again find, as in the case of steer A, that the first 3 days of period 2 (January 10–11, 11–12, and 12–13) contain a large excess of feces, actually amounting to 15.5 kg., which must represent the excretion of feces due to the more liberal ration of the preceding period.

With the curtailment of ration, smaller masses of feces per day were passed and, indeed, on the percentage basis wider fluctuations were observed, but this is not strange, since the alimentary tract of the steer is designed for large masses of fill, and the ration given curtailed the amount of fill to possibly one-half, thus involving a slower movement of feces inside the intestinal tract (because of its greater capacity for retention) and involving normally less regular defecation.

After the submaintenance ration the animals were given the original assumed maintenance amount (9.09 kg.) of hay for a period of 14 days only, from May 29 to June 12, during which time two collections of feces were unfortunately lost, i. e., on May 31–June 1 with steer A and on June 9–10 with steer B. With the increase in hay from 4,000 to 9,090 grams, the weight of fresh feces began almost immediately to increase, but at a somewhat different rate with the two animals. With steer A the fresh feces for May 28–29 were 7.75 kg., for May 29–30, 10.04 kg., and for May 30–31, 10.58 kg. The collection of feces was spilled on May 31–June 1. Thereafter the feces tended to increase steadily up to 15 or 16 kg. for the following 11 days. But with steer A, even at the end of 14 days, the original average fecal excretion of 19.18 kg. had not been reached. With steer B, on the other hand, the original average of 16.68 kg. was reached in 5 days. At the end of 2 weeks of increased hay feeding the animals were turned out to pasture. From the constantly increasing weights of the feces noted above, it is clear that during the 2 weeks of exclusively hay feeding there was a distinct accumulation of material which otherwise would normally have appeared in the feces. This has obviously been added to the fill. Because of the irregular feeding of these animals it is difficult to draw any direct comparisons with regard to the regularity and variability of defecation on the maintenance and on the submaintenance rations. On the one hand, irregularity in feeding, with the complete withdrawal of feed on certain dates, vitiates the comparative value of the normal fecal excretions. On the other hand, the great reduction in fill and the probability of retention of feces in the large alimentary tract promotes irregularity of expulsion of feces. The significant fact, however, is that nothing particularly abnormal appeared with regard to these feces, except that steers 8, 11, and B occasionally passed some mucus during the advanced stage of submaintenance.

When the fattening ration was given, i. e., in period 16, from December 3 to December 17, both animals showed a very large fecal excretion and, with the exception of the first 2 days with steer A, remarkably constant weights of feces from day to day.

### Physical Characteristics of Feces.

The most noticeable facts observed in connection with the feces of our cattle on reduced ration were the pronounced decrease in the total amount and particularly the greater firmness and shape of the feces on low feed-levels. Under normal conditions of feeding the feces were excreted in large, somewhat flattened, and almost plastic masses, but on submaintenance rations they were voided in small, almost round and hard lumps, which were more or less pilular and certainly gave the appearance of being very much less moist.[a] This was particularly apparent during the first year's work, when it became necessary to clean out the metabolism chamber after each respiration experiment with the animals. On the low ration the feces did not adhere to the woodwork, were very easily removed, and seemed much firmer. From the ocular evidence alone, therefore, one would expect to find that the feces had

[a] In the case of steer 12, on the tenth day of the submaintenance period the feces excreted were rather soft. This was the only exception noted.

measurably less water in them on the low ration. No analyses of feces for steers 1 to 12 were made, and consequently special attention was given to the collection, weighing, and analysis of feces with steers A and B. While the feces of steers 1 to 12 were perhaps somewhat denser, it is important to emphasize that they possessed the same characteristic with regard to lessened moisture and pilular form on the lower feed-level, as was observed with steers A and B. The protocols contain frequent records that the feces were voided in small, round balls, and were darker and harder than usual. It is also significant that a change in consistency was observed, even when the animals were starved for a respiration experiment; that is, when but two feeds equal to one day's ration were withheld, and when the animals were given extra feed after this short fasting to make up for that withheld prior to the chamber experiment, it was observed that the feces became softer. The feces, therefore, on the low ration were of themselves distinctly more solid and pilular in form than feces on ordinary full feed, and underwent a still further change in that they became denser under the conditions where short, complete withdrawals of feed were necessary.

Water intake apparently had a very marked effect on the feces, since it was observed in both years during the submaintenance periods that failure to drink on one day resulted in drier and darker feces on the following day, and that an unusual intake of water was manifested in somewhat softer feces on the following day. This was especially noticeable on the days following respiration experiments, when the steers subjected to the low feed-level, having had two feeds withheld, usually refused to drink.

The odors from feces during the submaintenance period were apparently no more marked than from those during the period of full maintenance, but during the heavy grain feeding the odors became particularly offensive.

### Chemical Composition of Feces.

The fresh feces for each of the 16 periods into which the observations with steers A and B were subdivided were weighed and the percentage of water-free substance determined in triplicate portions. In practically every instance the triplicate analyses agreed remarkably well, and hence in the final tabulation only the average results are given. The total nitrogen was likewise determined in triplicate in each of the 16 periods and on the fresh substance, to avoid loss of nitrogen by drying, and here also the triplicate analyses agreed well enough to permit the use of average values. To minimize somewhat the extensive chemical analyses that would otherwise be needed, we decided to subject only 5 samples of feces during the more typical series of experiments with steers A and B to the more complete determinations of ash, crude fiber, and ether extract. These determinations were made, therefore, only in periods 1, 3, 11, 13, and 16.[a] The percentages of water-free substance and of nitrogen, as recorded on the fresh basis, are given in Table 27, and the complete analyses of the feces for the 5 selected periods for each of the 2 steers, as expressed on the water-free basis, in Table 28.

[a] The determinations of water and total nitrogen and the more complete analyses were all made in the chemical laboratory of the New Hampshire State Agricultural Experiment Station under the direction of Dr. H. R. Kraybill, with the assistance of Mr. T. O. Smith. To both these gentlemen we are very much indebted for these painstaking analyses.

From the ocular observations with regard to the character of the feces as passed, special interest would be expected in the water determinations in the feces. The first 12 periods in Table 27 are periods in which hay alone was given. Of these periods it will be remembered that period 1 represented supposedly a maintenance ration, followed by 10 periods (2 to 11) with submaintenance feeding, and then by period 12, during which a maintenance ration was again fed as in period 1. Periods 13 to 16 were on fattening rations, including hay and concentrates. The lowest percentage of water-free substance in the first 12 periods with both steers was noted in period 1, namely, on the supposedly maintenance ration. In the case of steer A, 79.7 per cent of water was found in the feces on the average during the submaintenance periods and 82.6 per cent in the maintenance period, and with steer B the

TABLE 27.—*Percentage of water-free substance and nitrogen in fresh feces, steers A and B. (Average values.)*

| Period. | Date. | Water-free substance. | | Nitrogen. | |
|---|---|---|---|---|---|
| | | Steer A. | Steer B. | Steer A. | Steer B. |
| | 1919–20 | *p. ct.* | *p. ct.* | *p. ct.* | *p. ct.* |
| 1 | Dec. 27 to Jan. 10..... | 17.4 | 18.7 | 0.271 | 0.296 |
| 2 | Jan. 10 Jan. 24..... | 19.0 | 20.0 | .357 | .334 |
| 3 | Jan. 24 Feb. 7..... | 19.1 | 19.4 | .311 | .317 |
| 4 | Feb. 7 Feb. 21..... | 20.2 | 19.3 | .309 | .298 |
| 5 | Feb. 21 Mar. 6..... | 20.5 | 19.9 | .310 | .316 |
| 6 | Mar. 6 Mar. 20..... | 21.8 | 19.8 | .356 | .277 |
| 7 | Mar. 20 Apr. 3..... | 20.2 | 20.1 | .339 | .240 |
| 8 | Apr. 3 Apr. 17..... | 21.2 | 20.0 | .330 | .314 |
| 9 | Apr. 17 May 1..... | 18.4 | 19.4 | .318 | .335 |
| 10 | May 1 May 15..... | 21.2 | 20.6 | .336 | .315 |
| 11 | May 15 May 29..... | 21.4 | 20.3 | .321 | .304 |
| 12 | May 29 June 12..... | 18.4 | 19.3 | .282 | .248 |
| 13 | Oct. 22 Nov. 5..... | 22.4 | 20.3 | .348 | .410 |
| 14 | Nov. 5 Nov. 19..... | 17.3 | 19.8 | .341 | .400 |
| 15 | Nov. 19 Dec. 3..... | 15.5 | 19.5 | .357 | .524 |
| 16 | Dec. 3 Dec. 17..... | 16.9 | 19.6 | .395 | .560 |

percentage of water in feces during submaintenance was 80.1 on the average, as compared to 81.3 per cent in the maintenance period. It is, however, remarkable that such small differences in moisture-content should show such striking ocular differences in the character of the feces. On the resumption of fattening rations with concentrates, the percentage of water-free substance with steer A fell to a minimum of 15.5, while with steer B no essential change was noticeable throughout the entire year. Uncritical comparison of the last 4 periods between steer A and steer B may not be made, however, since steer B was distinctly on a high-protein ration, while steer A was on a low-protein ration. Prior to periods 13 to 16, however, both steers were given essentially the same amounts of hay in all periods.

The percentages of nitrogen for these periods are likewise incorporated in Table 27, from which it is seen that, in general, on the hay ration these animals show not far from about 0.3 per cent of nitrogen in the fresh feces.

The lowest value with steer A in period 1 is possibly to be accounted for by the fact that the percentage of water-free substance was lowest in this period. The same explanation does not hold true, however, for the lowest nitrogen percentage for steer B in period 7. During the last four periods, when concentrates were given, the differences in fecal nitrogen are more pronounced between the two animals, steer B on the high-protein ration excreting feces containing from 0.4 to 0.5 per cent or over of nitrogen in fresh material per day as compared to approximately 0.35 per cent with steer A. The chief significance of these figures, however, is that they throw light upon the question as to whether we are dealing here in any way with abnormalities in the composition of feces.

In spite, therefore, of the ocular impression that during the submaintenance periods the feces of the animals (not only steers A and B but likewise the animals on submaintenance rations in Groups II and III) were of a distinctly harder form, in smaller masses, and drier, we note from the analyses of the feces of steers A and B but little difference in the water-content, i. e., a difference of only 2 or 3 per cent.[a] It seemed entirely unnecessary to go through the literature for analyses of feces from exclusively hay rations, but from those tests that we have superficially examined it appears that the feces of steers A and B were well within any normal limits, so far as the moisture and nitrogen-content is concerned.

For a more complete study of the feces and of the possible influence of submaintenance periods we must turn to the more extended chemical analyses to which the feces were subjected in periods 1, 3, 11, 13, and 16. Since we have already considered the matter of water-content, these analyses, given in Table 28, are reported solely upon the water-free basis. For purposes of comparison, one analysis of feces reported earlier by Zuntz, and four analyses reported by Armsby and his associates are likewise included.

In considering these analyses in Table 28, it is important to recall that period 1 with both our animals, A and B, was supposed to represent maintenance feeding, periods 3 and 11 submaintenance (the submaintenance feeding having begun with period 2), and periods 13 and 16 heavy feeding with concentrates. The experimental defect in the use of the data for feces in period 1, namely, the absence of a sufficiently prolonged preliminary period of constant ration, has already been pointed out. Periods 3 and 11 fulfill very nearly the best specifications for collection of feces incidental to a digestion experiment, but periods 13 and 16 are again open to the criticism that the ration for the two weeks preceding was not identical with that during the feces collection.

The percentage of ether extract remains essentially constant with both animals in all periods. The percentage of crude fiber is essentially constant for all periods except the sixteenth, and the same is true with regard to the nitrogen. The percentage of nitrogen-free extract (which represents the

[a] Although Grouven's observations were made under conditions of extreme undernutrition, i. e., during fasting, it is important to note that with two different steers (see Grouven, loc. cit., pp. 147 and 149) he found during complete fasting a total fecal excretion of about 15 kg. for the first 5 days and, furthermore, found that the percentage of water decreased. Thus, the water-content of feces during the first and second days of fasting was 77.5 and 78.0 per cent, respectively, with 2 steers, while on the third and fourth fasting days it was 67.3 and 72.6 per cent, respectively. This decrease in the water-content of feces is quite in line with the tendency for slightly drier feces following restricted ration, as noted by us.

difference between 100 per cent and the sum of the percentages of the other constituents) shows somewhat wider variations, which are, however, in large part explained by the rather pronounced increase in the ash found in the last two refeeding periods. In general, the composition of the feces in periods 1, 3, and 11 (with a ration exclusively of hay) is practically constant with both animals.

TABLE 28.—*Chemical composition and energy value of water-free substance in feces of steers.*

(Benedict and Ritzman data compared with data of Armsby and Zuntz.)

| Animal and period. | Ash. | Ether extract. | Crude fiber. | Nitrogen. | Protein (N ×6.25). | Nitrogen-free extract. | Energy per gram of— | |
|---|---|---|---|---|---|---|---|---|
| | | | | | | | Water-free substance. | Water-free and ash-free substance. |
| Steer A[1]: | *p. ct.* | *p. ct.* | *p. ct.* | *p. ct.* | *p. ct.* | *p. ct.* | *cal.* | *cal.* |
| Period 1.. | 8.90 | 3.82 | 29.52 | 1.56 | 9.74 | 48.02 | 4.780 | 5.247 |
| Period 2.. | ..... | ..... | ..... | ..... | ..... | ..... | 4.807 | ..... |
| Period 3.. | 9.60 | 3.71 | 26.09 | 1.63 | 10.19 | 50.41 | 4.724 | 5.226 |
| Period 11.. | 8.52 | 3.52 | 26.43 | 1.50 | 9.36 | 52.17 | 4.804 | 5.252 |
| Period 13.. | 10.32 | 3.57 | 24.95 | 1.56 | 9.73 | 51.43 | 4.652 | 5.187 |
| Period 16.. | 11.06 | 3.25 | 23.43 | 2.34 | 14.62 | 47.64 | 4.555 | 5.121 |
| Steer B[1]: | | | | | | | | |
| Period 1.. | 8.74 | 3.96 | 29.88 | 1.59 | 9.91 | 47.51 | 4.740 | 5.194 |
| Period 2.. | ..... | ..... | ..... | ..... | ..... | ..... | 4.778 | ..... |
| Period 3.. | 9.24 | 3.74 | 26.69 | 1.63 | 10.21 | 50.12 | 4.839 | 5.332 |
| Period 11.. | 8.62 | 3.67 | 27.24 | 1.50 | 9.35 | 51.12 | 4.751 | 5.199 |
| Period 13.. | 11.28 | 3.52 | 26.07 | 2.02 | 12.63 | 46.50 | 4.615 | 5.202 |
| Period 16.. | 13.79 | 3.13 | 23.16 | 2.86 | 17.90 | 42.02 | 4.432 | 5.141 |
| Steer[2]: | | | | | | | | |
| Period 1.. | 11.20 | 6.07 | 23.15 | 1.83 | 11.42 | 48.16 | 4.693 | 5.285 |
| Steer A[3]: | | | | | | | | |
| Period III. | 5.67 | 2.12 | 39.94 | 1.38 | 8.61 | 43.66 | 4.861 | 5.153 |
| Period IV. | 5.63 | 2.11 | 41.08 | 1.30 | 8.10 | 43.08 | 4.791 | 5.077 |
| Steer B[3]: | | | | | | | | |
| Period III. | 5.87 | 2.18 | 38.52 | 1.58 | 9.88 | 43.55 | 4.894 | 5.199 |
| Period IV. | 6.50 | 2.05 | 39.55 | 1.53 | 9.58 | 42.32 | 4.833 | 5.169 |

[1] Benedict and Ritzman, experimenters.

[2] Zuntz, experimenter. See Von der Heide, Klein, and Zuntz, Landw. Jahrb., 1913, **44**, pp. 769 and 812. Animals fed hay only.

[3] Armsby, experimenter. See Armsby and Fries, U. S. Dept. Agric., Bureau Animal Industry, Bull. 128, 1911, p. 233; experiments in 1907. Animals fed hay only.

Although there are slight differences in the various chemical constituents, an examination of the heat of combustion on the water-free basis shows remarkable uniformity in the hay periods. Further information is also available on the heat of combustion, since it was determined directly on the feces for period 2, for which the other analyses were not available. It is seen, therefore, that the heat of combustion per gram of water-free substance in feces for periods, 1, 2, 3, and 11, is remarkably uniform for both animals.

In the fattening periods, 13 and 16, differences in chemical composition are instantly noted, particularly in the ash which is perceptibly higher with both animals in both periods. The percentage of ether extract remains essentially the same, with slightly lower figures in period 16 with both animals. The low value for crude fiber in the last period has already been cited. The percent-

age of nitrogen is higher in period 16, primarily because the ration contains a much larger proportion of nitrogen in the form of concentrates. The same necessarily applies to the protein, while the nitrogen-free extract is not far from that in the other samples. It is obvious, therefore, that in periods 13 and 16 the character of the feed has a distinct influence upon the feces, and there are hardly any differences between the two animals which are not fully accounted for by the changes in ration.

Since there was a pronounced difference in the amount of ash in the last two periods, it has been deemed important to compute the energy per gram on the water-free and ash-free basis, as given in the last column of the table for all specimens for which the ash was available, i. e., omitting period 2. On the water-free basis alone the energy per gram was lower in periods 13 and 16 with both animals than in the other periods, due in all probability to the distinctly higher ash-content, for when the computation is made on the water-free and ash-free basis we find a singularly uniform agreement between all the periods, save for a slightly lower value in the sixteenth period with both animals. The average heat of combustion on the water-free and ash-free basis for all 5 periods with steer A was 5.207 calories per gram and with steer B, 5.214 calories, an astonishingly close agreement. Furthermore, if we consider the widest deviations in the individual values from these averages (with steer B, for example, a range of from 5.141 to 5.332 calories), we find that the difference between the average value and either the minimum or maximum value is but about 2 per cent, and hence we can maintain that the energy per gram of water-free and ash-free substance in feces with these animals was within 2 per cent of the average for all 10 determinations.

In comparing the results of the analyses of the feces obtained with our animals with data secured from other animals on a ration exclusively of hay, namely, data from the laboratories of Zuntz and Armsby, we find that Zuntz reports for one of his steers an ash-content in feces which was higher than that noted by us in our periods with a ration exclusively of hay. Furthermore, he reports a value for ether extract nearly twice as high and for nitrogen slightly higher than our values. On the other hand, the heat of combustion per gram of water-free substance was almost the same as that found by us, namely, 4.693 calories, as compared with the average of 4.778 calories for all of our periods with an exclusively hay ration. Since the ash-content was so much higher, when we compute for Zuntz's steer the energy per gram of water-free and ash-free substance, we find very close agreement with our data, namely, 5.285 calories as against our grand average of 5.210 calories. With his steers A and B in periods III and IV, 1907, Armsby found a remarkably constant chemical composition of feces, so far as ether extract, nitrogen, and the energy per gram of water-free substance and per gram of water-free and ash-free substance is concerned. The heat of combustion on the water-free basis averages a little higher than our average, which is possibly to be accounted for by the fact that the ash-content was perceptibly lower than that found by us, for when the computation is made on the basis of water-free and ash-free substance, we find that Armsby's average of 5.150 calories is slightly less than our average of 5.210 calories.

In conclusion, it seems logical to infer that the great reduction in feed, which both of our animals experienced, had no appreciable influence upon the chemical composition of feces other than the tendency for the feces to be

slightly less moist in the low-ration periods. On the water-free basis, practically no change in composition can be observed in either of the samples of feces with steer A or steer B. It may be permissible, therefore, to conclude that the metabolic products (aside from undigested material in the feces) which are excreted along with feces must have represented essentially the same proportion of the total feces, irrespective of the alterations in ration.

Since in this report we are dealing primarily with the energy relations, it is important here to stress the significant fact that with these very wide ranges in ration, from an approximately one-half maintenance to a fattening ration, the heat of combustion of the feces per gram of water-free substance and particularly per gram of water-free and ash-free substance is under all these conditions remarkably constant. Hence it follows that by simple determination of the water in feces and by use of the factor 4.778 calories per gram of water-free substance, without chemical analyses or without the time-consuming calorimetric bomb tests one can compute from the water-free substance the heat of combustion of feces with great accuracy, an accuracy that can be but slightly improved by adding the ash determination to the water determination and making the computations upon the water-free and ash-free basis, using the factor 5.210 calories per gram of water-free and ash-free matter.

## DIGESTIBILITY OF THE RATIONS.

Presumably the digestive tract of an adult steer, which is very large and very complicated, is proportioned to the normal amount and bulk of feed which he would commonly consume at the various stages of growth. When the mass of feed material consumed is greatly reduced, as was the case with our adult steers on the curtailed rations, it is important to note whether this reduction has any effect upon the percentage of material actually absorbed or disappearing from the feed in its presumably slower passage through the digestive tract. In other words, digestion experiments with these steers at the different nutritive planes would have great value. In fact, the element of digestibility was a factor particularly considered in planning the second year's work in this general research, i. e., in the study with steers A and B. Ordinary feedstuffs were used, chiefly hay, together with certain concentrates. No particular difference is to be observed between the composition of these feedstuffs and those commonly grown on farms and found on the market. The actual chemical compositions of the hay and grains fed, so far as determined in connection with this research, are given in Table 2. (See p. 36.) From the determinations of the total water-free substance and nitrogen in feces in each of the 16 different periods with steers A and B, it is possible, knowing the water-free substance and nitrogen in the feed for the corresponding periods, to compute the so-called "digestibility"[a] of these two factors. Similarly, from the more detailed analyses of feed and feces for 5 of the 16 periods, we may compute the digestibility of the organic constituents and energy of the rations.

### Digestibility of Water-free Substance in Feed.

Perhaps the simplest method of determining the digestibility of these rations is to compare the total water-free substance in the ration with the water-free substance in the feces, thus securing a digestion coefficient of water-free substance. This has been done in Table 29, for steers A and B. Our great-

[a] For discussion of "digestibility" see Fries, Proc. Am. Soc. Anim. Produc., December, 1922, p. 33.

est interest in connection with this table is not in a comparison of these two animals, i. e., a study of individuality in digestion, but in a comparison of different periods, particularly in a comparison between the first and twelfth periods, which were supposedly maintenance, and the 10 periods between these, which were submaintenance.

TABLE 29.—*Digestibility of water-free substance in feed, steers A and B.*

| Period. | Steer and date. | Days. | Average daily water-free substance. | | |
|---|---|---|---|---|---|
| | | | (*a*) In feed. | (*b*) In feces. | (*c*) Digested $\left(\frac{a-b}{a}\times 100\right)$. |
| | 1919–20. | | | | |
| | Steer A: | | *kg.* | *kg.* | *p. ct.* |
| 1 | Dec. 27 to Jan. 7 | 11 | 6.88 | 3.56 | 48.3 |
| 2 | Jan. 10 Jan. 24 | 14 | 4.09 | 2.02 | 50.6 |
| 3 | Jan. 24 Jan. 31 | 7 | 4.10 | 1.54 | 62.4 |
| | Feb. 1 Feb. 7 | 6 | 4.10 | 1.76 | 57.1 |
| 4 | Feb. 7 Feb. 14 | 7 | 4.10 | 1.68 | 59.0 |
| | Feb. 15 Feb. 21 | 6 | 4.10 | 1.52 | 62.9 |
| 5 | Feb. 21 Mar. 6 | 14 | 3.81 | 1.65 | 56.7 |
| 6 | Mar. 6 Mar. 19 | 13 | 3.75 | 1.40 | 62.7 |
| 7 | Mar. 20 Mar. 26 | 6 | 3.61 | 1.45 | 59.8 |
| | Mar. 27 Apr. 3 | 7 | 3.61 | 1.40 | 61.2 |
| 8 | Apr. 3 Apr. 17 | 14 | 3.48 | 1.42 | 59.2 |
| 9 | Apr. 17 May 1 | 14 | 3.61 | 1.29 | 64.3 |
| 10 | May 1 May 6 | 5 | 3.61 | 1.54 | 57.3 |
| 11 | May 15 May 29 | 14 | 3.61 | 1.44 | 60.1 |
| 12 | June 1 June 12 | 11 | 7.83 | 2.86 | 63.5 |
| 13 | Oct. 22 Nov. 5 | 14 | 11.00 | 4.63 | 57.9 |
| 14 | Nov. 5 Nov. 19 | 14 | 13.78 | 4.52 | 67.2 |
| 15 | Nov. 19 Dec. 3 | 14 | 12.48 | 3.92 | 68.6 |
| 16 | Dec. 3 Dec. 17 | 14 | 12.98 | 3.96 | 69.5 |
| | Steer B: | | | | |
| 1 | Dec. 30 Jan. 9 | 10 | 6.54 | 3.14 | 52.0 |
| 2 | Jan. 10 Jan. 24 | 14 | 4.09 | 1.93 | 52.8 |
| 3 | Jan. 24 Feb. 7 | 14 | 4.05 | 1.63 | 59.8 |
| 4 | Feb. 7 Feb. 21 | 14 | 4.10 | 1.68 | 59.0 |
| 5 | Feb. 21 Mar. 6 | 14 | 3.81 | 1.59 | 58.3 |
| 6 | Mar. 6 Mar. 20 | 14 | 3.87 | 1.45 | 62.5 |
| 7 | Mar. 20 Apr. 3 | 14 | 3.61 | 1.44 | 60.1 |
| 8 | Apr. 3 Apr. 17 | 14 | 3.61 | 1.46 | 59.6 |
| 9 | Apr. 17 May 1 | 14 | 3.61 | 1.29 | 64.3 |
| 10 | May 5 May 15 | 10 | 3.61 | 1.45 | 59.8 |
| 11 | May 15 May 29 | 14 | 3.61 | 1.50 | 58.4 |
| 12 | May 29 June 9 | 11 | 7.83 | 2.72 | 65.3 |
| 13 | Oct. 23 Nov. 5 | 13 | 11.05 | 4.05 | 63.3 |
| 14 | Nov. 5 Nov. 11 | 6 | 14.02 | 5.36 | 61.8 |
| | Nov. 12 Nov. 19 | 7 | 14.79 | 4.77 | 67.7 |
| 15 | Nov. 19 Dec. 3 | 14 | 13.62 | 4.56 | 66.5 |
| 16 | Dec. 3 Dec. 17 | 14 | 13.29 | 4.98 | 62.5 |

With steer A it is seen that 48.3 per cent of the water-free substance in the feed was digested during the first or maintenance period. This percentage was increased to 50.6 during the transition period, namely, from January 10 to 24. From there on throughout the rest of the submaintenance period the percentages range from about 57 to 64, with no great tendency for regularity.

Assuming that the value for period 1 may be taken as a maintenance value (and this one may fairly question), it is clear that during the periods of low ration there is a noticeably higher percentage of water-free substance in the feed digested. Since one of the fundamental canons in digestion experiments was violated with these two animals, in that the first period was not preceded by 10 days or 2 weeks of constant feeding, the average water-free substance per day in feces during this period is, as has already been pointed out, probably somewhat too high for the feed given and represents some water-free substance from the preceding period, when a somewhat heavier ration was given. Under these circumstances, therefore, it would appear as if the amount of material remaining in the fill at the start of period 1 was really higher than it should be, that this excess was excreted during period 1, and that consequently the percentage of water-free substance apparently digested in this period is in reality somewhat higher than represented. The difference, therefore, between 48.3 per cent, which is the average value found in the first or maintenance period with steer A, and 59 per cent, which is the average value found in the 10 submaintenance periods following, i. e., a difference of about 11 per cent, may be at least partially wiped out by the inherent errors in the method of experimentation, so that we deal here not with so great an increase in digestibility on a submaintenance ration as seems apparent. Still, it is a question whether or not the *entire* difference would be wiped out.

The irregularities in this procedure are apparent the moment we compare the values found with steer B, for with this animal during the first period the digestibility of water-free substance amounted to 52 per cent, a value 4 per cent higher than that found with steer A. There is, however, an increase in digestibility of water-free substance in the periods of low ration with steer B also, the percentages actually reaching a point as high as 64.3, with an average of 59.

On the resumption of the maintenance ration of hay in period 12, the coefficient of digestion is 63.5 and 65.3 per cent for steers A and B, respectively, and during the fattening periods, i. e., the last 4 periods, this coefficient is not materially altered on the average with steer B, but it increases decidedly with steer A.

However, it is only to the rations exclusively of hay that particular interest is attached for the present, and in this connection the conclusion seems warranted that these animals show a somewhat higher digestibility of water-free substance on the low ration than they do in the one period of supposedly full maintenance. But in drawing this deduction, the fact must not be lost sight of that the maintenance period was probably in general too short and was unfortunately preceded by a somewhat varying feed level. Furthermore, the respiration experiments during the maintenance period made it imperative to withdraw feed for parts of certain days, thus necessarily complicating the problem of uniform feeding during this most important period. These considerations must inevitably vitiate any finality in conclusions based upon our digestion experiments.

On the other hand, attention is called to the fact that the variations found in the coefficients of digestion of total water-free substance during the hay periods are, in practically all cases, well within the ranges actually observed in other digestion experiments with hay, with the possible exception of the

value of 48.3 per cent noted in the first period with steer A. Waters[a] states that digestion experiments with some of his animals have indicated that there is a more complete digestion of the feed by the animal on a low nutritive plane. Moulton, referring undoubtedly to the same experiments which justified Waters's statement, gives some data for the percentage of total nutrients digested, from which he draws the conclusion that "It appears that in general the digestion coefficient increases as the plane of nutrition is lowered."[b] A strict comparison of these observations with our experiments can not be made, as the data with regard to the feed and feces analyses are not complete, but the general conclusion is quite in line with the inferences from the data in Table 29.

Armsby and Fries also contributed in a general way to this subject, in that they made a special study of the influence of the fatness of the animal upon the digestibility,[c] involving the feeding of light and heavy rations. They conclude that the digestibility of the lighter ration was greater than that of the heavier ration, although the difference was less than that usually found in such comparisons, the lighter ration showing a digestibility of dry matter but 2 per cent greater than the heavier ration.

### Digestibility of Organic Constituents and Energy of Feed.

While the discussion thus far has dealt solely with the digestibility of water-free substance, which for general purposes may be taken as more or less synonymous with the digestibility of organic matter, and particularly with the energy needed for the organism, a more subtle analysis of the character of the water-free substance is needed before drawing final conclusions. It is, therefore, necessary for us to examine the results for the special periods when the separate constituents in both feed and feces were determined.

One of the organic constituents, namely, the total nitrogen (from which the protein was computed by the use of the usual factors; see pp. 37 and 129) was determined in both feed and feces for all experimental periods. The results of these determinations are reported in Table 30, together with the coefficients of digestion of the nitrogen or crude protein. The nitrogen in feed naturally varied directly with the amount of water-free substance consumed in the hay periods, i. e., periods 1 to 12. In the refeeding periods large amounts of concentrates were given and in different proportions, steer B receiving much larger amounts of nitrogen than steer A. The percentages of digested nitrogen show a wide range, particularly with steer A, for in period 2 there was seemingly but 15.5 per cent of nitrogen digested by this animal, while in period 14 there was 56.2 per cent digested. With steer B, 28.0 per cent of the nitrogen was digested in period 2 and 74.2 per cent, the highest amount, in period 15.

In considering these coefficients of digestibility of nitrogen, attention must again be called to the inherent errors in the technique, namely, the lack of a prolonged preliminary period of uniform feeding prior to period 1, and particularly the sharp cut in ration at the beginning of period 2. Obviously the large fecal nitrogen in this second period, as compared to the succeeding periods, must be in considerable part explained by an expulsion of feces cor-

[a] Waters, Proc. 24th Annual Meeting Soc. Promotion Agric. Sci., 1908, p. 96.
[b] Trowbridge, Moulton, and Haigh, Univ. Missouri, Agric. Expt. Sta., Bull. 18, 1915, p. 19.
[c] Armsby and Fries, Journ. Agric. Research, 1917, 11, pp. 453 and 463.

responding to the ration level in the previous period, and consequently the coefficient of digestion is correspondingly lower. When the animals are upon an essentially uniform ration in periods 3 to 11, the coefficient of digestibility of nitrogen remains reasonably uniform with steer A, ranging only from 39.3 to 45.9 per cent. With steer B a considerably wider range is observed, particularly in periods 6 and 7, when the coefficient rises to 52.0 and 56.6 per cent, respectively. We have no adequate explanation for this unusually high digestibility in these two periods. On the fattening rations, great increases in digestibility of protein are observed, which are easily explainable on the ground that the coefficient of digestibility of the protein of concentrates is materially higher than that of hay.

TABLE 30.—*Digestibility of nitrogen in feed, steers A and B.* (*Average values per day.*)

| Period. | Date. | Nitrogen. | | | | | |
|---|---|---|---|---|---|---|---|
| | | Steer A. | | | Steer B. | | |
| | | (*a*) In feed. | (*b*) In feces. | (*c*) Digested $\left(\frac{a-b}{a}\times 100\right)$. | (*d*) In feed. | (*e*) In feces. | (*f*) Digested $\left(\frac{d-e}{d}\times 100\right)$. |
| | 1919–20 | *gm.* | *gm.* | *p. ct.* | *gm.* | *gm.* | *p. ct.* |
| 1 | Dec. 27 to Jan. 10 | 74.8 | 52.0 | 30.5 | 71.0 | 49.4 | 30.4 |
| 2 | Jan. 10 Jan. 24 | 44.7 | 37.8 | 15.5 | 44.7 | 32.2 | 28.0 |
| 3 | Jan. 24 Feb. 7 | 44.8 | 26.8 | 40.2 | 44.3 | 26.6 | 40.0 |
| 4 | Feb. 7 Feb. 21 | 44.8 | 24.5 | 45.3 | 44.8 | 25.9 | 42.2 |
| 5 | Feb. 21 Mar. 6 | 41.6 | 24.9 | 40.2 | 41.6 | 25.2 | 39.4 |
| 6 | Mar. 6 Mar. 20 | 42.3 | 22.9 | 45.9 | 42.3 | 20.3 | 52.0 |
| 7 | Mar. 20 Apr. 3 | 39.4 | 23.9 | 39.3 | 39.4 | 17.1 | 56.6 |
| 8 | Apr. 3 Apr. 17 | 38.0 | 22.0 | 42.1 | 39.4 | 22.9 | 41.9 |
| 9 | Apr. 17 May 1 | 39.4 | 22.3 | 43.4 | 39.4 | 22.3 | 43.4 |
| 10 | May 1 May 15 | 39.4 | 22.2 | 43.7 | 39.4 | 22.7 | 42.4 |
| 11 | May 15 May 29 | 39.4 | 21.6 | 45.2 | 39.4 | 22.4 | 43.2 |
| 12 | May 29 June 12 | 86.4 | 41.6 | 51.9 | 86.4 | 36.0 | 58.3 |
| 13 | Oct. 22 Nov. 5 | 151.3 | 72.0 | 52.4 | 244.0 | 81.6 | 66.6 |
| 14 | Nov. 5 Nov. 19 | 202.7 | 88.8 | 56.2 | 372.4 | 102.1 | 72.6 |
| 15 | Nov. 19 Dec. 3 | 203.1 | 90.5 | 55.4 | 475.4 | 122.5 | 74.2 |
| 16 | Dec. 3 Dec. 17 | 209.5 | 92.4 | 55.9 | 471.6 | 142.8 | 69.7 |

It is particularly unfortunate that the plan of the experiment was such as to leave quite uncertain the true influence of reduced ration upon the coefficient of digestibility of crude protein. From the figures in Table 30 it would appear as if there were a pronounced increase in the digestibility of this constituent. The criticism raised above, however, with regard to periods 1 and 2 is such as to invalidate this conclusion. Similarly, for period 12 the experimental data fail to give any definite information on this point. The increased hay ration in period 12 was accompanied by a great increase in the coefficient of digestibility of nitrogen, but this increase we believe is explained by retardation of expulsion of feces during period 12, due to the greater reserve capacity of the intestinal tract as a result of the previous low ration. In view of these considerations we must, therefore, conclude that, aside from the specifically high figures in periods 6 and 7 with steer B, there is nothing in

these results that implies any definite influence of undernutrition on the coefficient of digestibility of nitrogen.

The other organic constituents of the feed and feces, namely, crude fiber, ether extract, and nitrogen-free extract, as well as ash, and particularly the

TABLE 31.—*Digestibility of organic constituents, ash, and energy in feed, steers A and B. (Average values per day.)*

| Steer and period.[1] | Ash. | | | Ether extract. | | | Crude fiber. | | |
|---|---|---|---|---|---|---|---|---|---|
| | (*a*) In feed. | (*b*) In feces. | (*c*) Digested $\left(\frac{a-b}{a}\times 100\right)$. | (*d*) In feed. | (*e*) In feces. | (*f*) Digested $\left(\frac{d-e}{d}\times 100\right)$. | (*g*) In feed. | (*h*) In feces. | (*i*) Digested $\left(\frac{g-h}{g}\times 100\right)$. |
| Steer A: | *gm.* | *gm.* | *p. ct.* | *gm.* | *gm.* | *p. ct.* | *gm.* | *gm.* | *p. ct.* |
| Period 1 | 400 | 296 | 26 | 189 | 127 | 33 | 1,939 | 983 | 49 |
| Period 2 | ..... | ..... | ..... | ..... | ..... | ..... | ..... | ..... | ..... |
| Period 3 | 240 | 157 | 35 | 113 | 61 | 46 | 1,162 | 428 | 63 |
| Period 11 | 211 | 123 | 42 | 100 | 51 | 49 | 1,023 | 381 | 63 |
| Period 13 | 574 | 478 | 17 | 374 | 165 | 56 | 2,439 | 1,155 | 53 |
| Period 16 | 583 | 438 | 25 | 535 | 129 | 76 | 1,949 | 928 | 52 |
| Steer B: | | | | | | | | | |
| Period 1 | 380 | 273 | 28 | 179 | 124 | 31 | 1,842 | 932 | 49 |
| Period 2 | ..... | ..... | ..... | ..... | ..... | ..... | ..... | ..... | ..... |
| Period 3 | 237 | 151 | 36 | 112 | 61 | 46 | 1,148 | 435 | 62 |
| Period 11 | 211 | 129 | 39 | 100 | 55 | 45 | 1,023 | 409 | 60 |
| Period 13 | 663 | 457 | 31 | 420 | 143 | 66 | 2,584 | 1,056 | 59 |
| Period 16 | 832 | 688 | 17 | 688 | 156 | 77 | 2,303 | 1,156 | 50 |

| Steer and period.[1] | Protein. | | | Nitrogen-free extract. | | | Energy. | | |
|---|---|---|---|---|---|---|---|---|---|
| | (*j*) In feed. | (*k*) In feces. | (*l*) Digested $\left(\frac{j-k}{j}\times 100\right)$. | (*m*) In feed. | (*n*) In feces. | (*o*) Digested $\left(\frac{m-n}{m}\times 100\right)$. | (*p*) In feed. | (*q*) In feces. | (*r*) Digested $\left(\frac{p-q}{p}\times 100\right)$. |
| Steer A: | *gm.* | *gm.* | *p. ct.* | *gm.* | *gm.* | *p. ct.* | *cal.* | *cal.* | *p. ct.* |
| Period 1 | 467 | 324 | 31 | 3,846 | 1,600 | 58 | 30,547 | 15,917 | 48 |
| Period 2 | 279 | 236 | 15 | ..... | ..... | ..... | 18,266 | 9,710 | 47 |
| Period 3 | 280 | 167 | 40 | 2,305 | 827 | 64 | 18,311 | 7,747 | 58 |
| Period 11 | 247 | 135 | 45 | 2,030 | 751 | 63 | 16,122 | 6,918 | 57 |
| Period 13 | 924 | 450 | 51 | 6,691 | 2,381 | 64 | 49,087 | 21,539 | 56 |
| Period 16 | 1,254 | 579 | 54 | 8,659 | 1,887 | 78 | 58,201 | 18,038 | 69 |
| Steer B: | | | | | | | | | |
| Period 1 | 444 | 309 | 30 | 3,655 | 1,482 | 59 | 29,029 | 14,789 | 49 |
| Period 2 | 279 | 201 | 28 | ..... | ..... | ..... | 18,266 | 9,222 | 50 |
| Period 3 | 277 | 166 | 40 | 2,277 | 817 | 64 | 18,087 | 7,888 | 56 |
| Period 11 | 247 | 140 | 43 | 2,030 | 767 | 62 | 16,122 | 7,127 | 56 |
| Period 13 | 1,416 | 512 | 64 | 5,909 | 1,883 | 68 | 50,092 | 18,691 | 63 |
| Period 16 | 2,654 | 893 | 66 | 6,813 | 2,097 | 69 | 62,507 | 22,116 | 65 |

[1] Period 1, maintenance on hay alone; periods 2, 3, and 11, submaintenance on hay alone; periods 13 and 16, fattening on hay and grain.

total energy, were determined during periods, 1, 3, 11, 13, and 16. These determinations enable us to compute the coefficients of digestibility for each of the individual organic ingredients, the ash, and the energy. The results are recorded in Table 31. In any analysis of these digestion coefficients the criticism pertaining to the technique, and particularly to the results secured in period 1, obtains, that is, that owing to the somewhat heavier hay ration during the preliminary period there was undoubtedly a larger feces expulsion

than would normally accompany the ingestion of the feed given during period 1. Consequently one would, *a priori*, expect decreased coefficients of digestibility. This is particularly true in the case of protein (which has already been discussed as nitrogen[a] in Table 30) and energy, whose coefficients of digestibility were determined in period 2, the transition period. Both animals show that low coefficients of digestibility are found for all factors in the first period. In the second period low digestion coefficients are likewise found for nitrogen, protein, and energy. In periods 3 and 11, when the animals were upon a reasonably constant, though submaintenance ration, the coefficients rise perceptibly over those noted in period 1, agreeing reasonably well with each other in all instances, save for the coefficient of digestibility of ash with steer A, which was 35 per cent in period 3 and 42 per cent in period 11. Passing to the refeeding periods with the very great increase in feed in the form of concentrates, we find with steer A a lower digestibility of crude fiber in periods 13 and 16, with steer B also a lower digestibility of crude fiber in period 16 but practically no change in period 13, and with both animals a lower digestibility of ash and an increased digestibility of ether extract and nitrogen-free extract.

Emphasis has already been laid in this discussion upon the digestibility of protein, but for the special purpose of our research the proportion of total energy digested has greatest importance. Whatever variations there may be in the computed digestibility of the different individual constituents due to errors or irregularities in chemical analyses, these are ruled out in the case of the total energy digested, for this is based upon accurate determinations of the heat of combustion of feed and feces in the bomb calorimeter. Hence in studying the total energy digested, we have to deal primarily with physiological differences or with such technical errors as those already pointed out, namely, the too short preliminary feeding period and the inequality of the preceding ration, which affect particularly periods 1 and 2. If we consider now only the hay periods from 1 to 11, we find that the digestibility of energy is low in periods 1 and 2 and perceptibly higher in periods 3 and 11. With the realimentation and the use of concentrates, the proportion of energy digested increases in the last period with steer A and in both periods with steer B.

In this entire matter of digestibility, our special attention, however, deals with the hay periods. Since our experimental data are defective for a direct comparison of the digestibility of the individual constituents and the total energy between the so-called maintenance and submaintenance periods, we can only resort to a comparison of the digestion coefficients found with these animals and those obtained by other writers, particularly Armsby and his associates.[b] With two different animals, Armsby determined the coefficients of digestibility on both a submaintenance and a maintenance ration of timothy hay alone. His experiments, however, differ essentially from ours in that they were conducted in accordance with the best traditions of digestion experiments, namely, with long preliminary periods. But even with the discrepancies existing between Armsby's experiments and ours a direct com-

[a] Slight numerical differences are to be noted in the coefficients for digestibility of nitrogen and protein, since the protein was computed from nitrogen by the use of factors other than 6.25 in the case of the different grains. (See p. 37.)

[b] Armsby and Fries, U.S. Dept. Agric., Bureau Animal Industry, Bull. 128, 1911, Table 5, p. 27.

parison may be made, particularly for our periods 3 and 11, and such comparison shows that the coefficients of digestibility for practically all the individual constituents of the feed are well within the normal limits which may be said to have been established by Armsby's experiments. The crude-fiber digestibility of somewhat over 60 per cent noted with our two animals in periods 3 and 11 is, to be sure, much higher than that found by Armsby in his experiment with steer A in 1905 and 1906, i. e., 52.2 and 52.8 per cent, respectively, but is of the same order of magnitude as that found by him in 1907, i. e., 62.8 per cent. For the total energy, which is of greatest significance to us, the coefficient of digestibility for our steers is likewise essentially that found with Armsby's animals in 1907. In other words, a most careful comparison of our data with those so admirably obtained by Armsby fails to indicate any abnormality or any difference in digestibility that can be ascribed either to the submaintenance ration or to the individuality of the animals. Our conclusion must be, therefore, that the profound curtailment of ration did not measurably affect the coefficients of digestibility of the feed of our animals. The absence of positive evidence of an alteration in digestibility in our own animals is not inconsistent with the conclusions of Waters and Armsby, whose better plan in conducting experiments indicate a slightly increased digestibility with the lower nutritive plane. In any case, our digestion coefficients and those of Armsby differ by only a small per cent. The conclusion seems warranted, therefore, that the digestibility of a single feedstuff like hay is practically unaltered, either by the amount of hay fed, within wide limits, or the nutritive plane of the animal.

## URINE.

With but occasional lapses, the total amounts of urine for two of our steers, A and B, were collected for the entire period from December 27, 1919, to June 12, 1920. So far as we are aware, this is the longest continuous period in which animals of this size have been retained in metabolism stalls, with complete collection of urine and feces and complete measurement of feed and water. Under these conditions therefore, aside from the chemical composition of the urine, the actual weights of urine passed have more than ordinary significance.

### Variations in Urine Excretion from Day to Day.

With uniform feed intake, such as practically existed throughout the major portion of the time from December 27 to June 12, any influence of variation in quantity or quality of feed upon the amounts of urine excreted would be avoided. As is seen in Figs. 17 and 18 (pp. 86 and 87) where the daily weights of feed, water consumed, and feces and urine excreted are given for steers A and B, the individual daily weights of urine varied considerably, however, even when a uniform amount of feed was given. The two weeks from March 7 to 20, inclusive, represented in these charts came at about the middle of the submaintenance period and a sufficient length of time after the curtailment in ration for us to assume that the animals had passed through the transitory stage and had assumed their normal steady loss in weight due to the deficient ration.

With steer A the lowest value for urine excretion recorded in Fig. 17 is 1.2 kg., which occurs on March 8–9, and the highest value is 9.8 kg. on March 17–18. Of special note is the fact that for the first 3 days the urine excretion is at a relatively low level, approximately 2.5 kg., explainable in part perhaps by the fact that just prior to this period, on March 6, there was a respiration experiment with each animal, involving temporary withdrawal of feed. Hence steer A drank less water on March 5–6 and probably on March 6–7 (although the record for water consumption is missing on this day), and took no water at all on March 7–8. On March 10–11 there is an immediate increase in the urine excretion, the amounts remaining at an average of not far from 7.6 kg. for the remainder of the period. This weight more nearly represents the urine excretion under normal conditions without undue disturbance of feed intake, which indirectly reacts upon the amount of water taken. Still, since the withdrawal of feed before the respiration experiment and the disturbance in water consumption took place prior to the dates represented by these charts, it is only remotely possible that the low level of the urine excretion on the first few days is accounted for in any way by this prior disturbance in feed intake. Fig. 17 shows slight indications of an influence of drinking-water upon the amount of urine, although the peaks in the curve for urine do not by any means coincide with those for drinking-water.

Comparing the low level for the first 3 days, which may possibly be due to the prior disturbance in consumption of feed and drink, with the high level for the remainder of the period, which represents an unbroken, constant feed-intake until March 19 (when feed was withheld for another respiration experiment), we find no hint in the consumption of water to account for this increase in the urine excretion It is possible that the amount of feed, especially crude fiber, in the digestive tract may exert a tendency to retention and more even distribution of water than would be the case when the feed is withheld, as it was on the afternoon of March 5 and the morning of March 6. The data for steer B, which are given in Fig. 18, present a strikingly similar picture. On the first 3 days, as with steer A, the amounts of urine are low, a minimum of 1.9 kg. being recorded on March 7–8. On the fourth day there is a sudden increase to a very much higher level of about 8.9 kg. with a maximum of 11.0 kg. on March 17–18. A slight suggestion of the influence of large quantities of drinking-water upon the amounts of urine may be found in certain peaks of the two curves, but the simultaneous occurrence of the peaks is far from uniform and the deduction must be made that the relatively enormous changes in the amount of drinking-water have little, if any, immediate influence upon the weights of urine when animals are upon a constant hay ration.

The striking change in the amount of urine noted with both steers for the period after March 10, compared with the first part of the period (and it is to be observed that the urine curves can almost be superimposed), is very difficult of explanation other than that already offered as to the possible disturbance due to feed withdrawal on March 5–6. The previous records of urine excretion and water consumption for both these steers, as given in Fig. 23 (p. 140), show that the two animals were excreting urine in almost uniform amounts from February 21–22 to March 4–5, averaging about 5 kg. per day. The curve for the urine excretion of steer B stops at March 4-5, as the record for March 5–6 was lost. With steer A, since March 5–6 was a

fasting day, there was a tendency for the urine excretion to fall off on March 6–7, and a low level was reached on March 7–8, 8–9, and 9–10. The high amounts noted after March 9–10 in Figs. 17 and 18 can hardly be assumed as compensatory for the previous low values. The lack of uniformity between urine excretion and water consumption is strikingly shown in Fig. 23, for with both steers practically no close relationship between amount of water consumed and amount of urine excreted is to be noted. As has been pointed out before, these animals had a distinct tendency, especially when on low rations, to drink only on alternate days. The quantity of urine excreted, however, did not fluctuate in accordance with this practice. The striking increase in the amounts of urine from March 10 to the end of the period (shown in Figs. 17 and 18) is not attributable to any change in barn temperature nor to any alteration in ration, since the ration was constant at this

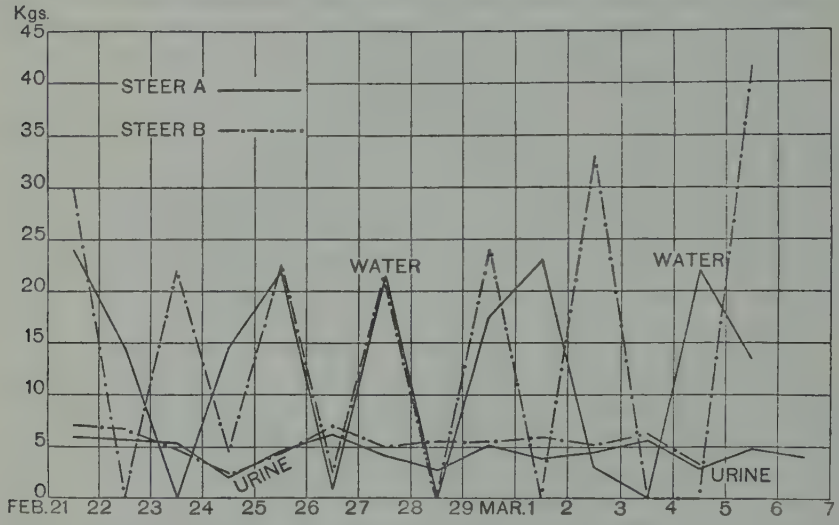


FIG. 23.—Curves for daily water consumption and urine excretion during 2 weeks on an essentially constant submaintenance ration of hay alone, steers A and B.

time, and we are entirely at a loss to account for this sudden and marked change in the quantity of urine excreted by both animals. The natural inference is that some factor which affected both animals came into play at this time. Disturbances in the feed-intake and the water-intake with subsequent excess feed might have caused a temporary retention of moisture, which was subsequently excreted. Our protocols give no evidence of any exciting activities at this time (such as, for example, construction or special activities in this section of the dairy barn) that would possibly stimulate a higher excretion of urine. It is, however, of very great significance that both animals show precisely the same phenomenon, this fact being of particular importance in the consideration of the use of two animals of this type as physiological duplicates, discussion of which is given subsequently. (See pp. 141 and 142.)

That no greater variations were observed in the amounts of urine voided by these animals from day to day is perhaps quite surprising, in view of the

fact that the collection of urine was made exactly at a given hour of the day, without reference whatsoever to the time of previous urination and the fact that the bladder might have been emptied immediately prior to the collection of the sample or several hours before. It is obvious that in a careful study of the daily excretion of urine the time of urination should be noted and, if possible, the volumes or weights of individual urinations. This procedure was beyond our experimental capacity at the time these studies were made. With humans, where separations can be made sharply and voluntarily, this problem does not enter. With smaller animals such as dogs, where catheterization can be employed, and with rabbits and guinea-pigs, where physical pressure upon the bladder may be relied upon to expel the urine, this factor does not enter, but with these large animals, where involuntary urination alone is possible, the problem of studying individual daily separations of urine is very complicated.

TABLE 32.—*Water-free substance in feed, water consumption, and urine and feces excretion, steers A and B (Average values per 24 hours.)*

| Period. | Date. | Steer A. | | | | Steer B. | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | Water-free substance in feed. | Water. | Urine. | Feces. | Water-free substance in feed. | Water. | Urine. | Feces. |
| | 1919–20. | *kg.* | *kg.* | *kg.* | *kg.* | *kg.* | *kg.* | *kg.* | *kg.* |
| 1 | Dec. 27 to Jan. 10.... | 6.84 | 26.0 | 5.0 | 19.2 | 6.50 | 24.5 | 6.0 | 16.7 |
| 2 | Jan. 10 Jan. 24.... | 4.09 | 12.5 | 4.0 | 10.6 | 4.09 | 15.0 | 4.8 | 9.6 |
| 3 | Jan. 24 Feb. 7.... | 4.10 | 12.5 | 5.0 | 8.6 | 4.05 | 11.0 | 5.4 | 8.4 |
| 4 | Feb. 7 Feb. 21.... | 4.10 | 12.5 | 5.0 | 7.9 | 4.10 | 13.0 | 6.1 | 8.7 |
| 5 | Feb. 21 Mar. 6.... | 3.81 | 12.5 | 4.5 | 8.0 | 3.81 | 14.5 | 5.3 | 8.0 |
| 6 | Mar. 6 Mar. 20.... | 3.87 | 11.0 | 6.1 | 6.4 | 3.87 | 12.5 | 6.3 | 7.3 |
| 7 | Mar. 20 Apr. 3.... | 3.61 | 14.0 | 6.2 | 7.0 | 3.61 | 15.0 | 6.8 | 7.1 |
| 8 | Apr. 3 Apr. 17.... | 3.48 | 11.0 | 4.4 | 6.7 | 3.61 | 12.0 | 5.1 | 7.3 |
| 9 | Apr. 17 May 1.... | 3.61 | 13.5 | 5.3 | 7.0 | 3.61 | 13.0 | 5.3 | 6.7 |
| 10 | May 1 May 15.... | 3.61 | 12.5 | 7.0 | 6.6 | 3.61 | 14.0 | 6.9 | 7.2 |
| 11 | May 15 May 29.... | 3.61 | 15.0 | 4.9 | 6.7 | 3.61 | 11.0 | 5.2 | 7.4 |
| | Total[1]..... | 44.73 | 153.0 | 57.4 | 94.7 | 44.47 | 155.5 | 63.2 | 94.4 |
| 12 | May 29 June 12.... | 7.91 | 22.0 | 4.5 | 14.7 | 7.91 | 21.5 | 5.4 | 14.5 |
| | Total[1]..... | 52.64 | 175.0 | 61.9 | 109.4 | 52.38 | 177.0 | 68.6 | 108.9 |
| 13 | Oct. 22 Nov. 5.... | 11.00 | 29.5 | 5.6 | 20.7 | 10.99 | 32.5 | 9.5 | 19.9 |
| 14 | Nov. 5 Nov. 19.... | 13.78 | 36.0 | 5.0 | 26.1 | 13.80 | 43.5 | 11.7 | 25.5 |
| 15 | Nov. 19 Dec. 3.... | 12.48 | 37.0 | 4.3 | 25.3 | 13.62 | 49.0 | 14.5 | 23.4 |
| 16 | Dec. 3 Dec. 17.... | 12.98 | 33.0 | 5.1 | 23.4 | 13.29 | 48.5 | 17.7 | 25.5 |

[1] Summation of average biweekly periods. Figures do not represent true totals.

## VARIATIONS IN AMOUNTS OF URINE FROM PERIOD TO PERIOD.

Although it has seemed impracticable to print the weights of urine and feces recorded for each experimental day throughout the entire winter with steers A and B, we have averaged these data by 14-day periods and present the averages in Table 32 together with the 14-day averages of the water-free substance in feed and the water consumed. In the first place, it is to be noted that the amounts of water-free substance in feed down to and including the

twelfth period were essentially the same with both animals. Water was furnished *ad libitum*, but the daily amounts were carefully recorded, and it can be seen that in general the same amounts of water were consumed in biweekly periods by both animals.

The uniformity of ration of these animals may be roughly shown by summing the average water-free substance in feed for periods 1 to 11. The total water-free substance may easily be computed by multiplying this result by the number of days in each period, i. e., 14, but this we have not done. The periodical average amounts per day for the first 11 periods total 44.7 kg. with steer A as against 44.5 kg. with steer B, thus indicating almost identical feed conditions. Since both animals were given the same average amount in period 12, namely, 7.9 kg., the evidence is clear that the ration condition for steers A and B was as nearly identical throughout the entire period of observation from periods 1 to 12, inclusive, as could be expected. Applying the same rough test of equality to the water consumption, by adding the biweekly figures, we get the arbitrary values of 153.0 kg. and 155.5 kg. with steers A and B, respectively, i. e., practical uniformity. In the twelfth period, when the hay ration was doubled, the steers both drank practically the same amount of water, i. e., 22.0 kg. and 21.5 kg., respectively. Adding the biweekly average values for the weights of feces, we find 94.7 kg. for steer A and 94.4 kg. for steer B for the first 11 periods, and if we include the twelfth period also, we find 109.4 kg. as against 108.9 kg. Therefore these two animals excreted essentially the same amounts of feces. With such uniformity in water-free substance in feed, water consumption, and weight of fresh feces, the difference in the amounts of urine excreted by the two animals is not to be disregarded. During the first 11 periods steer A almost invariably excreted less urine per day than steer B, the biweekly sums amounting to 57.4 kg. with steer A as against 63.2 kg. with steer B. Including the twelfth period, the biweekly sums are 61.9 kg. with steer A as against 68.6 kg. with steer B, indicating that steer B excreted 11 per cent more urine than did steer A.

The differences between the totals of intake and outgo for the individual biweekly periods are not pronounced, except for urine, with either of the animals during the first 12 periods, and it is with these periods that we are at present especially concerned, since they represent averages that tend to smooth over daily fluctuations caused by irregularity in retention of excreta. Steer A shows an extreme range in the biweekly average urine excretion from a minimum of 4.0 kg. to a maximum of 7.0 kg. With steer B the range is from 4.8 to 6.9 kg. It is worthy of note that practically the two highest values for steer A, namely, 6.1 and 6.2 kg., occur in the period selected for illustration, Fig. 17, in which connection it has already been pointed out that the high values on March 10 to 18 were especially prominent and probably significant. In other words, although the urine excreted during this period (as shown in this figure) started at the rather low level of about 2.5 kg. for the first 3 days, the change to a level of 7.6 kg. for the last 8 days (an amount 300 per cent greater) actually increased the total amount for the whole biweekly period itself over the preceding periods. It is also clear that the corresponding periods with steer B show high values, although absolutely the highest value occurs on May 1 to 15 with steer B, for which no special explanation is available.

### Influence of Water-free Substance in Feed on Amounts of Urine.

With the great change in the quantity of water-free substance in feed given these animals, due to the curtailment in ration from presumably full maintenance on hay in period 1 to about one-half maintenance on hay in the subsequent periods, we have ideal conditions for noting the influence, if any, of the amount of water-free substance in feed upon the weight of urine. With a full maintenance ration of hay in period 1 the average daily amount of urine was 5 kg. with steer A. In the 11 succeeding periods, when the hay ration was materially reduced, practically no change in the daily average quantity of urine was observed. In the case of steer B which had a daily average urinary excretion of 6 kg. on the maintenance ration, there was also practically no change on the greatly reduced ration, although almost invariably the amounts of urine were perceptibly larger than those noted with steer A. Thus it can be seen that a reduction of nearly 50 per cent in the water-free substance in feed on a ration exclusively of hay was practically without effect upon the amounts of urine excreted by both animals.[a]

The picture is altogether different, however, when we consider the fattening rations supplied both animals during the fall of 1920, after a period on pasture. With steer A the increase in the water-free substance in feed up to 13 or 14 kg. and in the water consumption up to as high as 36 or 37 kg. was essentially without influence upon the weight of urine. With steer B the increase in the water-free substance in feed was essentially that with steer A, although, as already pointed out, steer B was given a high-protein ration while steer A was given a low-protein ration. The water consumption was noticeably greater with steer B than with steer A. The feces excretion with both animals remained essentially equal, although markedly greater than in any of the preceding periods. But the striking difference is in the greatly increased amount of urine excreted by steer B. While in the first 12 periods steer B shows a relatively uniform urinary excretion of approximately 6 kg. daily, there is in the last 4 periods a continually increasing urinary excretion, beginning at a minimum of 9.5 kg. during period 13 and reaching a maximum of 17.7 kg. in period 16. Since the average daily amount of water-free substance in feed and the average daily weight of fresh feces remained essentially constant with both steers, it is quite clear that this difference in the amounts of urine excreted by the two animals must be accounted for probably in large part by the *character* of the ration.

### Nitrogen in Feed and Amount of Urine.

Because of the character of the ration, reference must be made to the amount of nitrogen in the feed, for the nitrogenous end-products of the feed digested and absorbed appear in the urine, and it is reasonable to suppose that with increased excretion of nitrogen there may automatically be an increased amount of urine. Accordingly, in Table 30 (see p. 135) we have recorded the average daily amounts of nitrogen in feed as well as the

[a] The low feed-level did, however, produce a marked change in the color and offensiveness of the urine, apparently as a secondary cause, by influencing directly the amount of water consumed. Thus, during the submaintenance period, when the water intake was markedly lower, the urine was of a much darker color and possessed a much more offensive odor. This was true with steers 1 to 12 as well as steers A and B.

percentages of digested nitrogen for both steers A and B. It is important, therefore, to consider the amounts of urine excreted in relation to the digested nitrogen. Identical treatment was accorded steers A and B up to June 12, under which conditions we note that, as pointed out in the discussion of digestibility, practically the same proportions of nitrogen were digested by both animals. Assuming for the moment that the animals were in nitrogen equilibrium, which was really far from the case, we can see from the digestion coefficients that there were rather material differences in the digestibility of the nitrogen in feed in the different periods, particularly in the second period, where the low value of 15.5 per cent was noted with steer A. In periods 6 and 7, when the amount of urine excreted by both animals was noticeably greater, we find nothing in the digestion coefficients for nitrogen to explain the high urine values for steer A, since 45.9 per cent in period 6 and 39.3 per cent in period 7 are essentially the average figures for digestibility of nitrogen with this animal. On the other hand, with steer B it is clear that there are noticeably higher figures for digestibility of nitrogen during periods 6 and 7. Indeed, the rather high figure of 56.6 per cent in period 7 might suggest some error in the weight of feces. All the data have been carefully scrutinized and checked without any hint as to the existence of such an error. The increased digestibility of nitrogen, therefore, in these two periods might possibly explain the increase in the urinary excretion of steer B.

In the four fattening periods (13 to 16, inclusive), the nitrogen in feed was very greatly increased, as was likewise the nitrogen in feces, with both animals. On the other hand, as seen in Table 32, the weight of urine with steer A was unaltered. The ingestion of this large amount of hay and grain therefore, of which approximately 55 per cent of the nitrogen was digested, had no influence upon the amount of urine excreted by steer A. The fattening ration of steer B contained very much larger amounts of nitrogen than that of steer A, and it was on the whole considerably better digested, the average digestion coefficient being nearer 71 than 55 per cent. This large amount of digestible nitrogen absorbed by steer B is coincidental with the noticeable increases in amounts of urine.

### Amount of Urine as Affected by Nitrogen in Urine.

On the supposition that the amount of urine will be determined in large part by the amount of excretory products to be discharged in it from the body, particularly nitrogenous products, an examination of the relationship between the total nitrogen excreted in urine and the weight of urine is necessary. The discussion of the total nitrogen in the urine as a factor in the nitrogen balance is to be shortly considered, but reference must be made here to data in Tables 34 and 35 (see pp. 148 and 149), in which are recorded, along with other data, the average amount of nitrogen excreted in the urine per 24 hours. These values are compared with the average daily weights of urine excreted (as given in Table 32, p. 141). Since the nitrogen in urine represents the metabolized nitrogen, we may disregard entirely the nitrogen intake and consider only the urinary nitrogen. In the first period the daily urinary nitrogen with steer A was 46.2 grams and with steer B 42.4 grams. From these amounts the excretions of both animals fall off with the succeeding periods of reduced ration, until an average minimum value of not far from 23 to 24 grams is

noted, steer B having a tendency for a slightly higher urinary nitrogen than steer A. These amounts of urinary nitrogen for periods 1 to 11, however, do not (as seen in Table 32), affect noticeably the weight of the urine. Likewise in period 12, with double the quantity of hay, the amount of urinary nitrogen and the total weight of urine remain practically unchanged.

When the fattening rations are given the situation is very different. With steer A an increase in urinary nitrogen from approximately 21 or 22 grams per day on the low rations to from 50 to as high as 89 grams per day on the fattening rations is without influence upon the average weight of urine. With steer B an increment in nitrogen from 24 grams during submaintenance to 125, 202, 285, and 308 grams daily during the four fattening periods, respectively, is accompanied by a very great change in urine volume. It is perhaps of singular note that the increase in urinary nitrogen from 21 grams to 89 grams in the case of steer A is without influence upon the weight of urine, while with steer B an increase of from 24 to 125 grams is accompanied by a change in weight of urine from 5.4 kg. to 9.5 kg. or about 80 per cent. The higher nitrogen figures with steer B are readily explained by the fact that this steer received the richer protein ration. From Tables 34 and 35 (pp. 148 and 149) it will be seen that the nitrogen in the ingesta was much higher in these last four periods with steer B than with steer A. Thus, steer A in the thirteenth period had 151 grams as compared with 244 grams received by steer B; in the fourteenth period he had 203 grams as compared with 372 grams by steer B; in the fifteenth period 203 grams as compared with 475 grams; and in the sixteenth period 209 grams as compared with 472 grams.

Perhaps the most remarkable observation in this analysis is the fact that on the ration of hay alone the amounts of urine were practically unaltered, irrespective of the amount of hay given, although the nitrogen in the hay in the first and twelfth periods was practically twice that in intermediate periods. The regulatory mechanism determining the secretion of urine by these animals is apparently unaffected by daily amounts of nitrogen in urine up to 90 grams per day.

### Nitrogen Metabolized.

The nitrogen in urine is taken as the nitrogen metabolized, though whether this is converted directly from food material or from body material it is impossible to state, save in long tests with accurate nitrogen balances. Obviously, only in the fasting state can the nitrogen metabolized be ascribed solely to a destruction of body material, although even during fasting with ruminants, as Grouven has so cleverly pointed out,[a] a considerable period of time elapses during which the large ballast or residue of partly digested feed in the fill is being drawn upon, so that the true fasting state is not reached until later. While the total urine passed by steers A and B was collected daily, with hardly a loss, from December 27 until June 12 and from October 22 to December 17, inclusive, it was impracticable to carry out analyses on all of these daily samples. Hence composite samples for every 2 weeks were made, the experiment between December 27, 1919, and December 17, 1920, aside from the period on pasture, being divided into 16 such biweekly periods.

[a] Grouven, Physiologisch-chemische Fütterungsversuche. Zweiter Bericht über die Arbeiten der agrikulturchemischen Versuchsstation zu Salzmünde, Berlin, 1864, p. 49.

The total nitrogen in urine has, therefore, been computed from the analyses of these composite samples, and the results are recorded, together with the body-weights, in Table 33. As a rough index of the feed consumed, we have also included in this table the water-free substance in feed, but it is important to keep in mind that during the first 12 periods the feed consisted exclusively of hay.

TABLE 33.—*Urinary nitrogen, steers A and B.*

| Period. | Date. | Steer A. | | | | Steer B. | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | Body-weight. | Water-free substance in feed. | Urinary nitrogen. | | Body-weight | Water-free substance in feed. | Urinary nitrogen. | |
| | | | | Total. | Per kg. of body-weight. | | | Total. | Per kg. of body-weight. |
| | 1919–20. | *kg.* | *kg.* | *gm.* | *mg.* | *kg.* | *kg.* | *gm.* | *mg.* |
| 1 | Dec. 27 to Jan. 10 | 600 | 6.84 | 46.2 | 76.9 | 567 | 6.50 | 42.4 | 74.8 |
| 2 | Jan. 10 Jan. 24 | 573 | 4.09 | 34.2 | 59.6 | 551 | 4.09 | 34.2 | 62.0 |
| 3 | Jan. 24 Feb. 7 | 555 | 4.10 | 31.6 | 57.0 | 538 | 4.05 | 31.4 | 58.4 |
| 4 | Feb. 7 Feb. 21 | 552 | 4.10 | 26.9 | 48.7 | 526 | 4.10 | 31.0 | 58.9 |
| 5 | Feb. 21 Mar. 6 | 538 | 3.81 | 24.0 | 44.6 | 510 | 3.81 | 28.3 | 55.5 |
| 6 | Mar. 6 Mar. 20 | 523 | 3.87 | 24.8 | 47.5 | 497 | 3.87 | 27.9 | 56.2 |
| 7 | Mar. 20 Apr. 3 | 517 | 3.61 | 25.1 | 48.5 | 488 | 3.61 | 25.6 | 52.5 |
| 8 | Apr. 3 Apr. 17 | 508 | 3.48 | 21.2 | 41.7 | 477 | 3.61 | 24.1 | 50.4 |
| 9 | Apr. 17 May 1 | 499 | 3.61 | 24.8 | 49.7 | 467 | 3.61 | 26.5 | 56.8 |
| 10 | May 1 May 15 | 488 | 3.61 | 22.2 | 45.4 | 456 | 3.61 | 22.8 | 50.0 |
| 11 | May 15 May 29 | 468 | 3.61 | 20.6 | 44.0 | 443 | 3.61 | 24.5 | 55.3 |
| 12 | May 29 June 12 | 496 | 7.91 | 21.0 | 42.3 | 465 | 7.91 | 23.9 | 51.4 |
| 13 | Oct. 22 Nov. 5 | 638 | 11.00 | 49.8 | 78.1 | 609 | 10.99 | 124.8 | 205.4 |
| 14 | Nov. 5 Nov. 19 | 659 | 13.78 | 68.0 | 103.2 | 634 | 13.80 | 201.9 | 318.5 |
| 15 | Nov. 19 Dec. 3 | 672 | 12.48 | 88.5 | 131.7 | 648 | 13.62 | 284.9 | 439.6 |
| 16 | Dec. 3 Dec. 17 | 681 | 12.98 | 89.4 | 131.3 | 663 | 13.29 | 308.4 | 465.2 |

During the first period, which was supposedly the maintenance period, the nitrogen metabolized per day averaged 46.2 grams with steer A and 42.4 grams with steer B, there being only a negligible difference between the two animals. To equalize the influence of differences in body-weights, we have computed the nitrogen metabolized per kilogram of body-weight, which we have also recorded in Table 33. According to this method of computation, the nitrogen metabolized amounted to 76.9 mg. with steer A in period 1 as against 74.8 mg. with steer B. Thus, on the basis of live weights, the difference between the two animals is essentially wiped out. This is all the more striking, however, when we consider that these figures represent a 2-week period with a ration exclusively of hay, preceded by a slightly heavier hay ration, and it is a matter of significance that both these large animals should have metabolized so nearly the same amount of nitrogen per kilogram of body-weight. In the succeeding periods, when the feed was cut by one-half, the nitrogen in urine shows a tendency to fall off during the first three or four periods, although the actual amounts in the urine per day are remarkably uniform for the second and third periods. Thereafter the urinary nitrogen remains reasonably constant with both animals, with a tendency for it to be somewhat higher with steer B. This higher value with steer B becomes somewhat more accentuated when the computations are based upon the nitrogen metabolized per kilogram of body-weight.

In the twelfth period, when a very greatly increased hay ration was given—indeed a ration which was even heavier in water-free substance than the ration in the first period—the total nitrogen excretion in the urine was unaffected in both animals. Since, however, the body-weights increased in both cases, the nitrogen metabolized per kilogram of body-weight underwent a perceptible drop in both cases.

That the increase in the water-free substance in the hay ration from 3.6 kg. in period 11 (corresponding to 39.4 grams of nitrogen) to 7.9 kg. (corresponding to 86.4 grams of nitrogen) in period 12 had no influence upon the total nitrogen in urine is indeed surprising. That a part of this increase simply went to augment the fill and hence practically did not enter into the metabolism of the body is highly probable. The remaining amount of nitrogen digested must have been so eagerly sought by the depleted body that the storage of nitrogen began immediately. It would appear, therefore, as if the nitrogen excretion of these animals was at about the minimum at this time. Indeed, from the data in Table 33 it appears that the total daily nitrogen excretion of these two animals (with an average body-weight of about 450 kg. and on a hay ration containing 3.6 kg. of water-free substance per day) was about 22 to 24 grams or 45 to 50 mg. per kilogram of body-weight.

The quantities of nitrogen thus metabolized with these steers were very low in the periods of reduced ration. Indeed an examination of practically all the current literature fails to show any prolonged nitrogen metabolism experiments with anything like as low nitrogen excretion as is noted with our animals, save in the extraordinary series of Grouven.[a] Rarely is a beef animal given a ration which results in such a low nitrogen excretion as was found with our animals, and in no instance, we believe, has an animal been subjected to a low ration such that the metabolism of nitrogen would be so low for a period of approximately 6 months.

## NITROGEN BALANCE.

A mere statement of the total nitrogen in urine or of the nitrogen metabolized per kilogram of body-weight can not possibly have the significance of a nitrogen balance, and hence it seemed necessary to determine the total nitrogen balance in these animals, that is, to compare the total nitrogen excreted in urine and feces with the nitrogen ingested in the feed. It is only from such a balance that one can estimate whether or not the animals are being given sufficient protein and calories to prevent prolonged, persistent drafts upon previously stored body-nitrogen. For this purpose, therefore, complete computations are necessary for the nitrogen of feed and the total nitrogen excreted in both urine and feces. As has already been shown, all

[a] The classical researches of Grouven in the original form are inaccessible to most readers but fortunately an admirable digest of his work has been prepared by Atwater and Langworthy (U. S. Dept. Agric., Office Expt. Sta., Bull. 45, 1898, pp. 288–293 and 299–300). According to this digest, the nitrogen in urine of two steers, weighing about 500 kg., was determined by Grouven in several 5- to 20-day experiments, when straw, water, salt, and sugar, and dextrins or gums alone were given. Values for urinary nitrogen were repeatedly found as low as 11 grams and, indeed, in one experiment as low as 8.6 grams. In this connection it is of interest, however, to note Grouven's important technique. He points out specifically (Grouven, loc. cit., p. 46) that in this series of experiments there was a great loss of flesh and fat during the periods of undernutrition, so that between each 2- and 3-week experiment it became necessary to give the animals liberal fattening rations to bring them back to their original weight.

three of these nitrogen values, namely, for feed, feces, and urine, were actually determined with steers A and B, and we have recorded the results in Tables 34 and 35 on the basis of average values per 24 hours for the different biweekly periods, together with the nitrogen balances computed therefrom.

The prime object of period 1 was to give these animals a ration that supposedly would provide for nitrogen and carbon or nitrogen and energy equilibrium, so that the animals could be said to be on a maintenance ration. Admittedly we were hurried in our work and made the error of assuming that reasonably constant body-weight through as short a time as 2 weeks was a correct index of equilibrium. In this supposition we simply followed the general custom in many digestion and metabolism experiments, and unless proof of equilibrium is established by metabolism and digestion experiments, all investigators are prone to fall into the same error. Thus, it was seen that our animals were far from being in equilibrium during period 1, as steer A

TABLE 34.—*Nitrogen balance, steer A.*

| Period. | Date. | Nitrogen intake per 24 hours in— | | | | Nitrogen excreted per 24 hours in— | | | Nitrogen balance per 24 hours. | Total loss or gain in nitrogen per period. |
|---|---|---|---|---|---|---|---|---|---|---|
| | | Hay. | Bran. | Corn-meal. | Total. | Urine. | Feces. | Total. | | |
| | 1919–20. | *gm.* | *gm.* | *gm.* | *gm.* | *gm.* | *gm.* | *gm.* | *gm.* | *gm.* |
| 1 | Dec. 27 to Jan. 10 | 74.78 | ..... | ..... | 74.78 | 46.18 | 51.96 | 98.14 | −23.36 | −327 |
| 2 | Jan. 10 Jan. 24 | 44.71 | ..... | ..... | 44.71 | 34.17 | 37.76 | 71.93 | −27.22 | −381 |
| 3 | Jan. 24 Feb. 7 | 44.80 | ..... | ..... | 44.80 | 31.63 | 26.77 | 58.40 | −13.60 | −190 |
| 4 | Feb. 7 Feb. 21 | 44.81 | ..... | ..... | 44.81 | 26.88 | 24.52 | 51.40 | − 6.59 | − 92 |
| 5 | Feb. 21 Mar. 6 | 41.61 | ..... | ..... | 41.61 | 23.99 | 24.88 | 48.87 | − 7.26 | −102 |
| 6 | Mar. 6 Mar. 20 | 42.26 | ..... | ..... | 42.26 | 24.84 | 22.93 | 47.77 | − 5.51 | − 77 |
| 7 | Mar. 20 Apr. 3 | 39.44 | ..... | ..... | 39.44 | 25.05 | 23.86 | 48.91 | − 9.47 | −133 |
| 8 | Apr. 3 Apr. 17 | 38.03 | ..... | ..... | 38.03 | 21.16 | 22.04 | 43.20 | − 5.17 | − 72 |
| 9 | Apr. 17 May 1 | 39.44 | ..... | ..... | 39.44 | 24.82 | 22.30 | 47.12 | − 7.68 | −108 |
| 10 | May 1 May 15 | 39.44 | ..... | ..... | 39.44 | 22.17 | 22.21 | 44.38 | − 4.94 | − 69 |
| 11 | May 15 May 29 | 39.44 | ..... | ..... | 39.44 | 20.58 | 21.57 | 42.15 | − 2.71 | − 38 |
| 12 | May 29 June 12 | 86.42 | ..... | ..... | 86.42 | 20.96 | 41.58 | 62.54 | +23.88 | +334 |
| 13 | Oct. 22 Nov. 5 | 94.82 | 26.12 | 30.39 | 151.33 | 49.84 | 71.95 | 121.79 | +29.54 | +414 |
| 14 | Nov. 5 Nov. 19 | 99.34 | 47.80 | 55.60 | 202.74 | 68.01 | 88.77 | 156.78 | +45.96 | +643 |
| 15 | Nov. 19 Dec. 3 | 60.46 | 65.94 | 76.70 | 203.10 | 88.49 | 90.45 | 178.94 | +24.16 | +338 |
| 16 | Dec. 3 Dec. 17 | 65.42 | 66.59 | 77.44 | 209.45 | 89.43 | 92.39 | 181.82 | +27.63 | +387 |

lost 23.4 grams of nitrogen per 24 hours throughout the entire period and steer B lost 20.8 grams, a total loss for the period of 327 grams with steer A and 291 grams with steer B. It has seemed unnecessary to attempt to apportion this loss of nitrogen to the probable total protoplasmic mass in the body. It was undoubtedly not a very large percentage loss to the body, but the fact that these animals were not securing sufficient feed to prevent a nitrogen loss is a serious defect in our experiments. This fact was not known until several months after the experiment was in progress, as it was impossible for us, with the pressure of other work, to carry out the analyses in time to make the computations and correct the error.

We should have profited by the experience of Armsby and Fries.[a] In discussing the use of a ration exclusively of hay they point out that timothy

[a] Armsby and Fries, U. S. Dept. Agric., Bureau Animal Industry, Bull. 51, 1903, p. 9.

hay was first selected by them as constituting a fairly definite farm product and also because of the somewhat greater simplicity of experiments with coarse fodder alone. This was an advantage which, however, had to be sacrificed later on account of the poverty of the hay in protein, for a preliminary digestion experiment revealed the low percentage digestibility of the protein and the unusual loss of nitrogen by the animal, showing that it would be necessary to add some nitrogen to the basal ration. They added a small amount of linseed meal.

TABLE 35.—*Nitrogen balance, steer B.*

| Period. | Date. | Nitrogen intake per 24 hours in— | | | | | Nitrogen excreted per 24 hours in— | | | Nitrogen balance per 24 hours. | Total loss or gain in nitrogen per period. |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Hay. | Bran. | Cotton-seed meal. | Lin-seed meal. | Total. | Urine. | Feces. | Total. | | |
| | 1919–20. | gm. | gm. | gm. | gm. | gm. | gm. | gm. | gm. | gm. | gm. |
| 1 | Dec. 27 to Jan. 10 | 71.02 | ..... | ..... | ..... | 71.02 | 42.40 | 49.42 | 91.82 | −20.80 | −291 |
| 2 | Jan. 10 Jan. 24 | 44.72 | ..... | ..... | ..... | 44.72 | 34.17 | 32.22 | 66.39 | −21.67 | −303 |
| 3 | Jan. 24 Feb. 7 | 44.25 | ..... | ..... | ..... | 44.25 | 31.43 | 26.55 | 57.98 | −13.73 | −192 |
| 4 | Feb. 7 Feb. 21 | 44.81 | ..... | ..... | ..... | 44.81 | 30.98 | 25.91 | 56.89 | −12.08 | −169 |
| 5 | Feb. 21 Mar. 6 | 41.61 | ..... | ..... | ..... | 41.61 | 28.32 | 25.21 | 53.53 | −11.92 | −167 |
| 6 | Mar. 6 Mar. 20 | 42.26 | ..... | ..... | ..... | 42.26 | 27.94 | 20.25 | 48.19 | − 5.93 | − 83 |
| 7 | Mar. 20 Apr. 3 | 39.44 | ..... | ..... | ..... | 39.44 | 25.60 | 17.10 | 42.70 | − 3.26 | − 46 |
| 8 | Apr. 3 Apr. 17 | 39.44 | ..... | ..... | ..... | 39.44 | 24.06 | 22.88 | 46.94 | − 7.50 | −105 |
| 9 | Apr. 17 May 1 | 39.44 | ..... | ..... | ..... | 39.44 | 26.54 | 22.27 | 48.81 | − 9.37 | −131 |
| 10 | May 1 May 15 | 39.44 | ..... | ..... | ..... | 39.44 | 22.79 | 22.66 | 45.45 | − 6.01 | − 84 |
| 11 | May 15 May 29 | 39.44 | ..... | ..... | ..... | 39.44 | 24.48 | 22.39 | 46.87 | − 7.43 | −104 |
| 12 | May 29 June 12 | 86.42 | ..... | ..... | ..... | 86.42 | 23.91 | 35.98 | 59.89 | +26.53 | +371 |
| 13 | Oct. 22 Nov. 5 | 94.28 | 26.12 | 74.21 | 49.40 | 244.01 | 124.81 | 81.63 | 206.44 | +37.57 | +526 |
| 14 | Nov. 5 Nov. 19 | 98.36 | 47.80 | 135.80 | 90.40 | 372.36 | 201.91 | 102.14 | 304.05 | +68.31 | +956 |
| 15 | Nov. 19 Dec. 3 | 64.36 | 71.70 | 203.70 | 135.60 | 475.36 | 284.85 | 122.49 | 407.34 | +68.02 | +952 |
| 16 | Dec. 3 Dec. 17 | 60.58 | 71.70 | 203.70 | 135.60 | 471.58 | 308.43 | 142.80 | 451.23 | +20.35 | +285 |

In our experiments one of the main objects was to carry animals through the winter on roughage at the lowest expense and to note the actual effect of such a procedure upon the animal body. We expected a pronounced loss in weight. We did not, however, realize that it was practically impossible to secure a maintenance ration for beef animals from a non-leguminous hay alone. While, therefore, in our first period, when the ration was supposed to be a maintenance one, there was a distinct loss in nitrogen, it is clear that this loss is wholly in accord with the experience of Armsby and Fries with hay alone. In their digestion experiment on hay alone, both animals weighed about 450 kg. or somewhat less than our steers A and B. Steer 1 received 6.804 kg. of hay per day and steer 2 received 5.443 kg. The nitrogen in the hay amounted to 48.73 grams with steer 1 and 38.98 grams with steer 2, or 44 grams on the average, an amount essentially that given in our submaintenance periods, and yet both animals lost per day 6.95 and 9.07 grams of nitrogen, respectively. The fact that with even 70 to 75 grams of nitrogen in the hay in our so-called "maintenance period" there was a large nitrogen-loss per day speaks again for the difficulties of securing nitrogen equilibrium with hay alone.

With the pronounced cut in the hay ration of our steers, when the nitrogen intake in period 2 was reduced to 44.7 grams in both cases, a loss in nitrogen occurred, as was to be expected, amounting on the average to 27.2 and 21.7 grams per day with steers A and B, respectively. It was pointed out in discussing the digestibility, that during period 1 both animals were upon a somewhat lower nutritive plane than they were prior to this period, which means that unquestionably some of the feces excreted during this time were feces more properly belonging to a previous period representing a somewhat heavier ration. Any method of computation, therefore, involving the use of the data for feces in period 1, would tend to lower markedly the percentage value for the digestibility of the hay, as pointed out in an earlier section, and in this particular case to accentuate the loss in nitrogen. Thus, in all probability the true amount of nitrogen in the fecal excretion, with a ration containing 70 to 75 grams of nitrogen in the hay, would be somewhat less than 52.0 grams with steer A and 49.4 grams with steer B. Every gram of nitrogen in the feces thus wrongly introduced into the calculation of the nitrogen-loss makes the deficit too large, and in all probability the daily loss in period 1 was less than the 23.4 and 20.8 grams recorded in Tables 34 and 35. How much should be deducted from these amounts it is impossible to state, owing to the difficulty of determining exactly the changes in fill. Similarly, in period 2 the animals suddenly underwent a very great change in the nutritive plane, the amount of nitrogen in the feed being only about two-thirds that in period 1. There was unquestionably some fecal nitrogen in period 2 that should more properly be chargeable to the ration of period 1, and hence the actual computed loss in nitrogen is somewhat accentuated but to what extent one can not definitely state. This holds true for both animals.

The fecal excretion of nitrogen, however, practically reached the low value ascribable to the low hay ration during the third period with both steers A and B, and we can definitely assume that the nitrogen deficit of 13.6 and 13.7 grams in the two animals during the third period is a reasonably true measure of the nitrogenous loss. This loss continued through the eleventh period, although at not quite so high a level, and, indeed, with a tendency for the level to decrease progressively. In the twelfth period, when the nitrogen in the ration was again increased (being, as a matter of fact, somewhat greater than it was during period 1), there was no change in urinary nitrogen, as already shown, but there was a pronounced change in the fecal nitrogen and a resulting plus in the nitrogen balance amounting to about 25 grams with both animals. Here again, however, exactly the same criticism applies as was made of the balances struck in periods 1 and 2, namely, that the true nitrogen balance is obscured by the effect of the change in fill and the resultant change in fecal nitrogen, only here in the reverse order. In period 12, with steer A the fecal nitrogen was almost double that in period 11, but unquestionably, since this was a transition period, the fecal nitrogen was not so large as it would be somewhat later when equilibrium could be established, so that 42 grams represents somewhat too low a figure. For the moment one may compare this value with the value of 52 grams noted during period 1 on a noticeably lower hay ration. With steer B the fecal nitrogen increased from 22.4 grams in period 11 to 36 grams in period 12, but still was not so large as the 49.4 grams found in period 1. While, therefore, change in fill undoubtedly

affected the fecal nitrogen in both periods 1 and 2, thus making the apparent nitrogen deficit too large, the change in fill and the change in fecal nitrogen unquestionably had the reverse effect in period 12 in making the seeming plus balance too low.

This analysis of the nitrogen balances only accentuates again the difficulties of making digestion experiments with ruminants unless they are preceded by relatively long periods of uniform feeding, to establish digestive equilibrium. It also accentuates the great importance of a chemical and microscopical study of fill with animals slaughtered in different nutritive conditions, and the desirability of studying in even shorter periods the transitions from one plane of nutrition to another.

Between periods 12 and 13, i. e., from June 13 to October 21, inclusive, the animals were on pasture and their metabolic history is entirely unknown other than that they gained materially in weight. The last weight before going to pasture was 515 kg. for steer A and 471 kg. for steer B, and the first weights on returning from pasture were 632 kg. and 601 kg., respectively. Steer A therefore gained 117 kg. and steer B 130 kg. It is highly probable that considerable additions to the nitrogen in the body took place during the pasture period, although no measurement was made of the nitrogen metabolism at this time. With the feeding of concentrates, the whole picture of the nitrogen balance is fundamentally altered. In the first place, there was a very great increase in the nitrogen intake, as shown in the first half of Tables 34 and 35. Secondly, as we have already pointed out, there was a great increase with both animals in the urinary and fecal nitrogen. That much higher figures are found with steer B than with steer A for both total nitrogen in urine and nitrogen per kilogram of body-weight is easily explained by the fact that the nitrogen in the ration of steer B was much higher than in that of steer A.

With the fattening rations given in the last four periods, the consistent nitrogen-loss noted in periods 1 to 11 now becomes definitely converted into a plus balance. A plus balance is, indeed, indicated during period 12, but in periods 13 to 16 it is as a rule greater than in period 12, thus showing a pronounced storage of nitrogen throughout this time. When we consider that between periods 12 and 13 there was a long interval of grazing with every probability of a considerable replenishment of the depleted nitrogen, the high capacity for storage of nitrogen in these last four periods is all the more pronounced. With steer A the period averages for plus nitrogen balances range from 24 grams in period 15 to 46 grams in period 14. Referring to the nitrogen in the intake, it can be seen that these plus balances are not invariably proportional to the nitrogen intake, for with steer A in periods 15 and 16, when the nitrogen in the intake amounted to 206 grams, the plus balance was about 26 grams, while in period 14, with practically the same amount of nitrogen in the feed, the plus balance was almost twice as great. Steer B, having the higher protein intake, shows balances singularly enough nowhere near as much greater than steer A as one would expect. The nitrogen in the intake with steer B is essentially twice that with steer A, indeed, somewhat more than twice on the average, while the plus balances range only from 20 grams in period 16 (an average daily balance actually lower than any noted in the last four periods with steer A), to a maximum of 68 grams

for periods 14 and 15. Apparently, therefore, even with the excessively high protein in the ration furnished steer B, the actual addition of nitrogen was nowhere near as great proportionately as would perhaps be expected. The important point, however, is that with the resumption of grain feeding all the balances become positive and in an appreciable degree, so that we have clearly to do here with an anabolic process resulting in the addition of protein to the body and probably simultaneously large amounts of fat, as a result of the fattening ration.

### Total Loss of Nitrogen during the Period of Underfeeding and Subsequent Gain of Nitrogen with Fattening Rations.

It is important to obtain some conception of the total loss of nitrogen from the body during these periods of undernutrition. For this purpose we have simply taken the average value for each biweekly period, as given in the next to the last column of Tables 34 and 35, and multiplied it by 14, thus recording in the last column of the tables the sum total of the loss in nitrogen for each biweekly period from December 27 to May 29, inclusive. From these computations we note that on May 29, that is, at the end of period 11, steer A had shown a total loss of 1,589 grams of nitrogen, while steer B had shown a total loss during the same period of 1,673 grams of nitrogen. During the next 2 weeks steer A gained 334 grams, which meant that up to the moment of going to pasture he had a total deficit of 1,255 grams of nitrogen. Steer B during the same period had gained 371 grams, which made his total loss up to the time of going to pasture 1,302 grams. A knowledge of the gain of nitrogen during the pasture season would of course have been extraordinarily valuable. It is highly probable that a large part, if not the whole, of this loss was made up during the somewhat over 4 months on pasture and, indeed, probably additions were made thereto. The increases in body-weight would certainly speak for a probable compensation of the deficit.

During the period of fattening, when metabolism measurements were carefully made, it can be seen that there were very heavy additions to the nitrogen in the body, for in the two months from October 22 to December 17 steer A had added 1,782 grams of nitrogen to the body, while steer B, on a considerably heavier nitrogen ration, had added 2,719 grams. During periods 13 to 16, steer A increased in weight about 55 kg. and steer B about 65 kg. According to the common methods of computation,[a] the 1,782 grams of nitrogen gained by steer A during this period would correspond to about 10.7 kg. of protein and this in turn to about 43 kg. of flesh. In this case we can see that even with steer A, which showed the lowest gain of protein, the nitrogen (expressed as flesh) added during this period would account for nearly the entire gain in body-weight, while with steer B it is quite obvious that the weight of flesh (65 kg.) computed from the nitrogen gained would be the same as the entire gain in weight. It is highly probable that the well-known difficulties of securing exact uniformity in fill and water-content make an exact comparison under these conditions somewhat hazardous, but it would seem as if there had been a heavy storage of flesh during periods 13 to 16. On the other hand, the addition of organized nitrogenous material to the

[a] Assuming that each gram of nitrogen added to the body represents 6.0 grams of dry protein and that there are 4 grams of water combined with every gram of protein to form flesh.

adult animal body is usually considered to take place only with great difficulty, and one would expect that the increase in weight, especially during the grain period, was in large part an addition of fat. Actual analyses of the carcasses at the end of the study would have been valuable, and this whole phase of the investigation is extremely suggestive of problems regarding the true addition of nitrogenous tissue to a previously starved or depleted organism. Finally, in any consideration of the storage or loss of nitrogen under these conditions, the hypothesis advanced in connection with a similar loss of nitrogen from the body in the case of some young men,[a] namely, that we have to deal not so much with a loss of organized flesh as with a withdrawal of nitrogenous material dissolved in the body fluids, should be carefully considered. For the purpose of the calculations above it has been assumed that each gram of nitrogen corresponds to 24 grams of flesh. If the nitrogen is to be added in the form of a soluble protein even larger proportions of water might be needed to hold it in solution. Careful chemical analyses of body-fluids and particularly the muscle-juices under these conditions alone can contribute to this phase of the physiology of the animal.

Although the influence of the striking difference in the quantity of protein in the ration upon the relative gains in body-weight by steers A and B should be considered fully as much as the influence of such a difference upon the gains in nitrogen, this latter point is well illustrated in Tables 34 and 35. With steer A there was an actual storage of nitrogen from October 22 to December 17, inclusive, of 1,782 grams, which involved the ingestion of 10,732 grams of nitrogen during the corresponding period, or each gram of nitrogen stored necessitated the ingestion in the form of hay and grain of 6 grams of nitrogen, while with steer B during this period there was a storage of 2,719 grams, but an ingestion of 21,887 grams, or 8 grams of nitrogen were ingested for every gram of nitrogen stored. Thus, on this basis alone, the storage of protein with steer B was less economical than it was with steer A, although the ration of steer B was much richer in protein than that of steer A.

Any fixed conclusions, however, from this inspection of the nitrogen stored on these different rations are much complicated by the fact that undoubtedly both animals were losing nitrogen prior to the beginning of the maintenance period. They had been on hay for some time before that, and all the evidence is to the effect that it is practically impossible to secure a nitrogen balance on hay alone. Consequently the total nitrogen-losses shown by these animals are minimum, for they should be increased by the losses which they had suffered prior to the beginning of the maintenance period.

### Correction for Loss of Nitrogen in Epidermal Tissue.

In any critical analysis of a nitrogen balance one may not simply compare the nitrogen of the income in the shape of hay and concentrates with the nitrogen of the urine and feces, for while under ordinary conditions this relationship is very close, there is a continuous loss of nitrogen taking place through the growth of hair and dandruff which should be taken into consideration. Indeed, in the careful experiments carried out by Professor Armsby, the nitrogen lost through this source is regularly considered. Thus

[a] Benedict, Miles, Roth, and Smith, Carnegie Inst. Wash. Pub. No. 280, 1919, pp. 353 and 354.

in his admirable study on the utilization of feed by cattle, as determined by their degree of fatness, Professor Armsby,[a] with characteristic accuracy, determined and used in his calculations the nitrogen lost through the epidermal tissue. As a matter of fact, with the particular steer studied he found that the growth of hair resulted in a loss of nitrogen from the body of 0.4 gram per day, while in the brushings or combings there was a loss of 1.8 grams, making a total daily correction of 2.2 grams for the nitrogen represented in the production of epidermal tissue. A loss of 2.2 grams of nitrogen per day in epidermal tissue with a daily nitrogen excretion in urine amounting to from 79.5 to 155.6 grams, as in the experiments of Armsby referred to, is not an appreciable percentage of the total nitrogen-loss. When, however, the daily excretion of nitrogen in urine is as low as 22 grams, as it was in several biweekly periods with both steers A and B, it can be seen that a daily loss of 2.2 grams in the epidermal tissue may amount to 10 per cent of the total urinary loss of nitrogen and hence should not be neglected.

Unfortunately we did not realize the significance of this fact sufficiently to measure the nitrogen lost in this way by our animals. Perhaps we unconsciously felt that we could safely rely upon the many figures secured by Professor Armsby. In fact, our entire study is so fundamentally based upon his capital researches that we were perhaps, if anything, too prone to accept standard figures from his laboratory rather than secure our own. Be that as it may, such measurements can not be disregarded in careful nitrogen balances. The situation is directly comparable to many observations of the loss of nitrogen through the skin with humans. Hundreds of nitrogen metabolism experiments with men have been made and the computations of nitrogen balances given to milligrams, with utter disregard of the normal amount of nitrogen lost through the skin, a loss which may amount to 0.3 gram per day or more with humans.[b] In our own experiments with steers A and B, it is quite clear that a daily addition of 2 grams to the nitrogen loss would in the course of 154 days, i. e., 11 periods of 14 days each, increase the deficit by 308 grams. If we consider that the total gain in nitrogen shown by both animals in period 12 practically offsets this addition to the deficit, we can see that the total loss up to the time of going to pasture was 1,589 grams with steer A and 1,673 grams with steer B.

Of course, it is not impossible that on the low nutritive plane there may have been a decreased formation of epidermal tissue accompanying the generally lowered metabolic activity. Subsequent experiments at Durham with animals actually fasting seem to indicate, however, that there is, if anything, an increased loss of hair. In any event it is safe to conclude that throughout the entire period of pasture and the subsequent fattening periods the epidermal loss of nitrogen continues at not far from the rate of 2 grams per day. Under these conditions, therefore, all of the average losses (given in Tables 34 and 35) must be increased by this amount and the apparent plus balances must similarly be decreased at the rate of 2 grams per day. This correction does not, to be sure, alter fundamentally the deduction raised in the foregoing paragraphs as to the storage of considerable masses of protein material in the body and the fact that the nitrogen stored in the form of

[a] Armsby and Fries, Journ. Agric. Research, 1917, 11, p. 468.
[b] Benedict, Journ. Biol. Chem., 1905, 1, p. 263.

flesh corresponds approximately to the actual gain in weight of the animals during the last four periods.

The importance of the estimate of the loss of hair was noted by Grouven.[a] With three different steers he found a seasonal variation in loss of hair, the loss being larger, i. e., about 5 grams of hair[b] per day, during February, March, and April than during the other nine months, i. e., 2 grams of hair per day. If we make a rough assumption, according to Grouven's data, that there is 17 per cent of nitrogen in the hair, it can be seen that there would be a daily loss of about 0.9 gram of nitrogen in the hair during the months of February, March, and April. While it is of great interest to find that Grouven realized, as early as 1864, the importance of noting the loss of nitrogen by this channel, it is obvious that the more accurate figures, which include the nitrogen of dandruff and epidermal tissue in general, as presented by Dr. Armsby, more nearly represent the true epidermal loss.

## METABOLIZABLE ENERGY.

Although each different ingredient in the feedstuffs has its special significance when one is considering particularly the matter of digestibility and the rapidity of absorption and utilization of feed in the body, the main interest in a study of undernutrition, such as is here undertaken, is not the fate of the individual nutrients but the energy relationships. We may consider the energy relationships from the general standpoint of energy utilizable in the body, the energy from all the various nutrients being pooled, as it were. Obviously the potential energy of feces must be deducted from the energy of feed before any approximation of the true energy available to the body can be made. The digestible energy, namely, the difference between the energy of the feed and the energy of the feces, is not, however, the true measure of the total energy of the feed that is available to the body to sustain life, for in addition to the excretion of unoxidized organic material in the feces, there is a not inconsiderable loss of unoxidized material in the urine, such as urea and, particularly with herbivora, hippuric acid. Moreover, the extensive fermentative processes in the large alimentary tract of ruminants result in the production and escape of considerable amounts of methane, with its potential energy. To express that portion of the energy of feed that may ultimately be used by the body in its various energy transformations, at the same time making proper allowance not only for the energy lost in feces, but likewise for the potential energy of urine and the energy lost in the fermentative processes, the term "metabolizable energy" has been introduced by Armsby. This term means that proportion of the energy of the feed which may be used by the body in its life processes and which, reduced to its simpler terms, corresponds to energy of feed less energy of feces, urine, and methane.

### Computation of the Metabolizable Energy, Group IV.

The metabolizable energy is relatively simply computed by deducting from the gross energy of feed the energy of feces, urine, and methane. This com-

[a] Grouven, loc. cit., pp. 81 and 82.

[b] Daily loss of nitrogen from shedding hair is of course not proportional to the nitrogen diverted by the body daily for hair-growth, since the latter is a slow process, whereas shedding the full-length hairs (especially during seasonal shedding) represents a greater sum total of nitrogen.

putation expresses the amount of energy that the animal body can use, but, as Armsby has so well pointed out, involves no explanation of the method by which it will be used or the efficiency with which it will be used. Of our 14 steers, animals A and B (Group IV) were the only ones with which sufficient data were accumulated to make possible the direct calculation of the metabolizable energy. With these two animals the energy in feed and feces was actually determined in a calorimetric bomb, but the energy in urine and in methane had to be computed.

### ENERGY IN METHANE.

The peculiar processes of fermentation in the intestinal tract of ruminants have been studied extensively, and it is usually assumed that the chief gases resulting from this fermentation are carbon dioxide and methane. It is obviously impracticable to collect the methane, and hence experimenters have had to resort to the determination of this constituent in the air of respiration chambers, measuring it quantitatively and computing from the known heat of combustion of methane the loss of energy involved in this process of fermentation. In determining the methane, samples of air are first freed from carbon dioxide and are then passed over some oxidizing mixture, such as copper oxide or, more commonly, platinized asbestos or kaolin, and the resulting carbon dioxide and water formed are collected and weighed. The ratio of carbon to hydrogen in the molecule of methane is 2.976 to 1, while the average of 57 experiments reported from Armsby's laboratory[a] showed a ratio of 3.167 to 1 with considerable variations in individual cases. Armsby is inclined to think that the high figure was due to a failure to oxidize the last traces of hydrogen in the combustion-tube. If free hydrogen were produced in the process of fermentation, one would normally expect a ratio low rather than high, and yet a number of researches from Zuntz's[b] laboratory have apparently shown the presence of free hydrogen under the conditions of fermentation taking place in the intestinal tract. On the other hand, so careful a worker as Krogh[c] was unable to detect hydrogen, and he believes that earlier reports of its presence in fermentative processes in the paunch of the steer are attributable to experimental errors.

Our apparatus at Durham was not provided with means for measuring the methane. A close examination of the extensive series of measurements made by Armsby and his associates led us to believe that this was an unnecessary refinement and complication. It is, however, very important to have some reasonably close estimate of the amount of methane formed under the conditions of our experiments. Fortunately, thanks to Armsby's researches, we are in a position to compute by two different methods the loss of energy due to the production of methane. In the first place, Armsby has found that on rations exclusively of timothy hay there is a production of methane amounting on the average to an energy loss of 331 calories per kilogram of water-free substance in the hay.[d] The individual experiments show such uniform agreement with this general figure that we feel perfectly justified in applying it to our hay experiments. Armsby's results also show that there

[a] Armsby and Fries, Journ. Agric. Research, 1915, 3, p. 439.
[b] Von der Heide, Klein, and Zuntz, Landw. Jahrb., 1913, 44, p. 765.
[c] Krogh and Schmit-Jensen, Biochem. Journ., 1920, 14, p. 686.
[d] Armsby and Fries, Journ. Agric. Research, 1915, 3, p. 441.

are produced on the average 4.5 grams of methane for every 100 grams of digested carbohydrates,[a] with an energy loss of 13.344 calories per gram of methane.[b] These latter values are practically independent of the character of the feeding-stuff and hence give a second method of computing the energy in methane and, indeed, with mixed rations. Both methods of computing the energy in methane have been employed in our research. Thus, when the ration consisted exclusively of hay, as it did in periods 1 to 12 with steers A and B, the factor 331 calories per kilogram of water-free substance in hay has invariably been used. In the refeeding periods, 13 to 16, the factors suggested by Professor Armsby of 4.5 grams of methane per 100 grams of digested carbohydrates and 13.344 calories per gram of methane were used.

The amount of digested carbohydrates could readily be computed for periods 13 and 16 since (as is seen in Table 28, p. 129) complete analyses were made of the feces excreted in these periods. From an analysis of the hay and the assumed compositions of the grains, it was possible to compute the carbohydrates of the feed and from the analyses of the feces the undigested carbohydrates. For periods 14 and 15 analyses of the feces were not made. With steer B, however, it was found that the ratio between the amount of digestible carbohydrates and the carbohydrates in feed was practically the same in periods 13 and 16. Therefore, in periods 14 and 15 it seemed justifiable to compute the amount of digestible carbohydrates from the carbohydrates in the feed, by interpolation of the values for periods 13 and 16. With steer A this ratio between the amount of digestible carbohydrates and carbohydrates in feed in periods 13 and 16 did not agree so closely and interpolation of the values for use in periods 14 and 15 did not seem to be justifiable. By reference to Table 31 (p. 136) it was found that the percentage of digestible crude fiber in periods 13 and 16 was practically identical, i. e., 53 and 52 per cent, respectively, so it was decided to assume that for periods 14 and 15 the amount of crude fiber digested would be 53 per cent of the amount of crude fiber in the feed eaten. In the case of nitrogen-free extract it was found that 64 per cent was digested in period 13, while 78 per cent was digested in period 16. Since in period 16 there were 8,659 grams of nitrogen-free extract in the hay and grain, while in periods 14 and 15 there were 8,702 and 8,367 grams, respectively, it was decided that periods 14 and 15 corresponded more closely to period 16 than to period 13 (with only 6,691 grams of nitrogen-free extract in the feed), and accordingly it was assumed that the amount of nitrogen-free extract digestible in periods 14 and 15 would be 78 per cent of the nitrogen-free extract in feed eaten in these periods. Addition of the computed amounts of digestible crude fiber and nitrogen-free extract of course gave the total digestible carbohydrates for these periods.

Thus it is seen that two distinctly different methods were employed for computing the energy of methane in the experiments with steers A and B, (1) on the basis of the water-free substance in hay alone (i. e., in periods 1 to 12, inclusive), by using the factor 331 calories per kilogram of water-free substance in hay, and (2) on the basis of the digestible carbohydrates in the mixed rations (i. e., in periods 13 to 16, inclusive), by using the factors suggested by Dr. Armsby of 4.5 grams of methane per 100 grams of digestible

[a] Armsby and Fries, Journ. Agric. Research, 1915, 3, p. 451.
[b] Armsby, Nutrition of farm animals, New York, 1917, p. 636.

carbohydrates and 13.344 calories per gram of methane. Both methods are undoubtedly sufficiently accurate for the computation of the energy of methane under the conditions of our experiments. Indeed, a comparison of the two methods is not without interest, and in Table 36 we have therefore given this comparison for periods 1, 3, and 11, on the ration exclusively of hay. The agreement between the two methods, particularly in periods 3 and 11, is most satisfactory. In period 1, where the agreement is less close, it must be borne in mind that the method of determining the digestible carbohydrates is open to criticism, due to the fact that the preliminary feeding period prior to period 1 was unsatisfactory, and we believe that in this period it is better to use the results based upon water-free substance in hay. For the refeeding periods the computation of energy in methane is based exclusively, as already stated, upon the amount of digestible carbohydrates.

TABLE 36.—*Comparison of energy in methane as computed from water-free substance in hay and from digested carbohydrates.*

| Steer and period. | From water-free substance in hay. | From digested carbohydrates. |
|---|---|---|
| | *cal.* | *cal.* |
| Steer A: | | |
| Period 1..... | 2,264 | 1,923 |
| Period 3..... | 1,357 | 1,328 |
| Period 11..... | 1,195 | 1,153 |
| Steer B: | | |
| Period 1..... | 2,152 | 1,851 |
| Period 3..... | 1,341 | 1,305 |
| Period 11..... | 1,195 | 1,128 |

## ENERGY IN URINE.

While the direct determination of the energy of feed and feces in the calorimetric bomb presents no particular technical difficulties and is not liable to any serious error other than the possible loss of organic matter in the drying of feed, and particularly in the drying of feces, the determination of the energy in urine is somewhat difficult, for, in the first place, one has a large volume of liquid to reduce to a sufficiently dry form to burn in the bomb. In this process there may be a volatilization of organic matter including a loss of ammonia, which also has a certain potential energy. To complicate our technique by the direct determinations of the energy lost in urine in each period was impossible with the experimental facilities available, but fortunately we were able again to rely upon the mass of experimental evidence furnished by Professor Armsby and his associates. Based upon the fact that the energy in urine under certain conditions bears a reasonably close relationship to the nitrogen in urine, this ratio has been carefully determined under a large number of feeding conditions and may be used for the computation of the loss of energy in urine, without introducing serious error.

When animals are upon a submaintenance ration exclusively of hay, it has been found that each gram of nitrogen in the urine is accompanied by a loss of about 22 calories, while on a maintenance ration of hay alone each gram of nitrogen in the urine is accompanied by a loss of approximately 30

calories. These two factors are derived from the extensive reports of Professor Armsby and his associates,[a] and it is our special pleasure to record that we have enjoyed the experience of Professor W. W. Braman of the Pennsylvania Institute of Animal Nutrition, who has been good enough to select these as the most probable constants for use under the conditions of our experiments. Accordingly in periods 2 to 11, inclusive, we have employed the factor of 22 calories per gram of urinary nitrogen and in period 12 the factor of 30 calories. In period 1 we employed the factor of 22 calories rather than 30 calories, because the ration during this period was not, strictly speaking, a maintenance ration. When fattening rations are given, with mixed feeds, the amount of energy lost per gram of nitrogen in urine decreases very noticeably, and consequently in the fattening periods, 13 to 16, we have used for the constant 12.63 calories per gram of nitrogen, based upon a research with heavy rations by Armsby and his associates.[b]

The computation by these factors of the energy lost in the urine does give, it is true, a very close estimate of the total potential energy in the urine. It is important to note, however, that of this energy in the urine a certain part may come not from feed but from katabolized body material, if the animal is losing nitrogen during the period, as indeed was the case with our 2 animals for the first 11 periods. Since our immediate problem is to compute the metabolizable energy derived from the feed, it is obvious that a correction is necessary here for the energy lost in the nitrogen of urine resulting from the katabolism of flesh. According to Rubner,[c] the potential energy of the urine is increased by about 7.45 calories for each gram of urinary nitrogen coming from the oxidation of body-protein. That is, when the body draws upon its own material for energy, it is impossible for it to burn completely all the energy in the body flesh, and with each gram of nitrogen broken down and excreted as partially oxidized material in the urine, 7.45 calories are lost. Therefore, in periods 1 to 11, with our 2 animals, when minus nitrogen balances were observed, nitrogen was being lost from the body in the urine, with a resultant loss of 7.45 calories for each gram of nitrogen lost. Consequently the total amount of nitrogen excreted in the urine in periods 1 to 11 represents nitrogen coming both from the feed and from body material, and after multiplying the urinary nitrogen by the factor 22, the amount of energy due to body-nitrogen should be *subtracted* from the total energy of urine, because the energy in this body-nitrogen was not derived from energy in the feed consumed. In periods 12 to 16, on the contrary, plus nitrogen balances are shown, and in these cases there is a storage of nitrogen in the body derived from the feed eaten. Consequently, the total nitrogen in urine should be multiplied by the factor 30 in period 12 and by 12.63 in periods 13 to 16, to obtain the energy due to urinary feed-nitrogen and to this energy of feed-nitrogen in urine should be *added* the energy due to the flesh stored (body-nitrogen multiplied by 7.45 calories), because this body-nitrogen in these cases has been derived from the feed eaten.

Unfortunately, in all of this consideration of the correction for the storage or loss of nitrogen in our experiments, we are face to face with the fact that,

[a] Armsby and Fries, U. S. Dept. Agric., Bur. Anim. Indus., Bull. 128, 1911.
[b] Armsby and Fries, Journ. Agric. Research, 1917, 11, Table V, p. 454.
[c] Rubner, Zeitschr. f. Biol., 1885, 21, pp. 316 and 329; ibid., 1901, 42, p. 303.

owing to too short preliminary feeding affecting period 1 and to tremendous transitions in the quantity of the rations during periods 2 and 12, it is doubtful whether these computations hold to the fullest extent with periods 2 and 12 and possibly with period 1. As we have fully considered this error of technique in other parts of the report, it seems unnecessary to do more than point out here the fact that this error probably enters to a greater or less extent into a true calculation of that portion of the urinary nitrogen whose energy should be subtracted from the energy of feed in the computation of the metabolizable energy. Since the correction is at best but a relatively small proportion of the total energy of urine and an almost insignificant fraction of the total metabolizable energy of feed, we have not deemed it advisable to go further into this treatment, and consequently the computations as made do not make any allowance either for the continuously decreasing feed in the period preceding period 1 or for the alterations in feed and fill incident to periods 2 and 12.

## Metabolizable Energy on Hay Rations, Group IV.

The calculations of metabolizable energy for steers A and B (Group IV) are given in Table 37. The determined energy in feed and feces and the com-

Table 37.—*Metabolizable energy in feed, steers A and B. (Average values per day.)*

| Steer and period. | Date. | Feed. | | Feces. | | |
|---|---|---|---|---|---|---|
| | | (a) Water-free substance. | (b) Energy.[1] | (c) Fresh. | (d) Water-free substance. | (e) Energy.[1] |
| Steer A: | 1919–20. | *kg.* | *cal.* | *kg.* | *kg.* | *cal.* |
| 1 | Dec. 27 to Jan. 10.... | 6.84 | 30 547 | 19.18 | 3.33 | 15,917 |
| 2 | Jan. 10 Jan. 24.... | 4.09 | 18,266 | 10.59 | 2.02 | 9,710 |
| 3 | Jan. 24 Feb. 7.... | 4.10 | 18,311 | 8.61 | 1.64 | 7,747 |
| 4 | Feb. 7 Feb. 21.... | 4.10 | 18,311 | 7.94 | 1.61 | 7 693 |
| 5 | Feb. 21 Mar. 6.... | 3.81 | 17,015 | 8.04 | 1.65 | 7,884 |
| 6 | Mar. 6 Mar. 20.... | 3.87 | 17,283 | 6.44 | 1.40 | 6,689 |
| 7 | Mar. 20 Apr. 3.... | 3.61 | 16,122 | 7.03 | 1.42 | 6,785 |
| 8 | Apr. 3 Apr. 17.... | 3.48 | 15,542 | 6.67 | 1.42 | 6,785 |
| 9 | Apr. 17 May 1.... | 3.61 | 16,122 | 7.01 | 1.29 | 6,164 |
| 10 | May 1 May 15.... | 3.61 | 16,122 | 6.62 | 1.40 | 6,689 |
| 11 | May 15 May 29.... | 3.61 | 16,122 | 6.72 | 1.44 | 6,918 |
| 12 | May 29 June 12.... | 7.91 | 35,326 | 14.72 | 2.71 | 12,948 |
| 13 | Oct. 22 Nov. 5.... | 11.00 | 49,087 | 20.71 | 4.63 | 21,539 |
| 14 | Nov. 5 Nov. 19.... | 13.78 | 61,611 | 26.06 | 4.52 | 20,589 |
| 15 | Nov. 19 Dec. 3.... | 12.48 | 55,975 | 25.31 | 3.92 | 17,856 |
| 16 | Dec. 3 Dec. 17.... | 12.98 | 58,201 | 23.42 | 3.96 | 18,038 |
| Steer B: | | | | | | |
| 1 | Dec. 27 to Jan. 10.... | 6.50 | 29,029 | 16.68 | 3.12 | 14,789 |
| 2 | Jan. 10 Jan. 24.... | 4.09 | 18,266 | 9.64 | 1.93 | 9,222 |
| 3 | Jan. 24 Feb. 7.... | 4.05 | 18,087 | 8.37 | 1.63 | 7,888 |
| 4 | Feb. 7 Feb. 21.... | 4.10 | 18,311 | 8.68 | 1.67 | 7,979 |
| 5 | Feb. 21 Mar. 6.... | 3.81 | 17,015 | 7.97 | 1.58 | 7,549 |
| 6 | Mar. 6 Mar. 20.... | 3.87 | 17,283 | 7.32 | 1.45 | 6,928 |
| 7 | Mar. 20 Apr. 3.... | 3.61 | 16,122 | 7.13 | 1.43 | 6,833 |
| 8 | Apr. 3 Apr. 17.... | 3.61 | 16,122 | 7.28 | 1.46 | 6,976 |
| 9 | Apr. 17 May 1.... | 3.61 | 16,122 | 6.65 | 1.29 | 6,164 |
| 10 | May 1 May 15.... | 3.61 | 16,122 | 7.20 | 1.48 | 7,071 |
| 11 | May 15 May 29.... | 3.61 | 16,122 | 7.37 | 1.50 | 7,127 |
| 12 | May 29 June 12.... | 7.91 | 35,326 | 14.50 | 2.80 | 13,378 |
| 13 | Oct. 22 Nov. 5.... | 10.99 | 50,092 | 19.93 | 4.05 | 18,691 |
| 14 | Nov. 5 Nov. 19.... | 13.80 | 63,625 | 25.54 | 5.04 | 22,337 |
| 15 | Nov. 19 Dec. 3.... | 13.62 | 63,974 | 23.36 | 4.56 | 20,210 |
| 16 | Dec. 3 Dec. 17.... | 13.29 | 62,507 | 25.50 | 4.99 | 22 116 |

TABLE 37.—*Metabolizable energy in feed, steers A and B. (Average values per day.)*—Continued.

| Steer and period. | Date. | Urine. | | | (*i*) Energy in methane.[4] | Metabolizable energy per day. | | |
|---|---|---|---|---|---|---|---|---|
| | | (*f*) Nitrogen. | (*g*) Nitrogen balance. | (*h*) Energy.[3] | | (*j*) Total [*b*−(*e*+*h*+*i*)] | Per kg. water-free substance in feed. | |
| | | | | | | | (*k*) By periods (*j*÷*a*) | (*l*) Average periods 3 to 11. |
| Steer A: | 1919–20. | *gm.* | *gm.* | *cal.* | *cal.* | *cal.* | *cal.* | *cal.* |
| 1 | Dec. 27 to Jan. 10.... | 46.18 | −23.36 | 842 | 2,264 | [5]11,524 | 1,685 | |
| 2 | Jan. 10 Jan. 24.... | 34.17 | −27.22 | 549 | 1,354 | [5]6,653 | 1,627 | |
| 3 | Jan. 24 Feb. 7.... | 31.63 | −13.60 | 595 | 1,357 | 8,612 | 2,100 | |
| 4 | Feb. 7 Feb. 21.... | 26.88 | − 6.59 | 542 | 1,357 | 8,719 | 2,127 | |
| 5 | Feb. 21 Mar. 6.... | 23.99 | − 7.26 | 474 | 1,261 | 7,396 | 1,941 | |
| 6 | Mar. 6 Mar. 20.... | 24.84 | − 5.51 | 505 | 1,281 | 8,808 | 2,276 | |
| 7 | Mar. 20 Apr. 3.... | 25.05 | − 9.47 | 481 | 1,195 | 7,661 | 2,122 | 2,131 |
| 8 | Apr. 3 Apr. 17.... | 21.16 | − 5.17 | 427 | 1,152 | 7,178 | 2,063 | |
| 9 | Apr. 17 May 1.... | 24.82 | − 7.68 | 489 | 1,195 | 8,274 | 2,292 | |
| 10 | May 1 May 15.... | 22.17 | − 4.94 | 451 | 1,195 | 7,787 | 2,157 | |
| 11 | May 15 May 29.... | 20.58 | − 2.71 | 433 | 1,195 | 7,576 | 2,099 | |
| 12 | May 29 June 12.... | 20.96 | +23.88 | 807 | 2,618 | [5]18,953 | 2,396 | |
| 13 | Oct. 22 Nov. 5.... | 49.84 | +29.54 | 850 | 3,359 | 23,339 | 2,122 | |
| 14 | Nov. 5 Nov. 19.... | 68.01 | +45.96 | 1,201 | 4,924 | 34,897 | 2,532 | |
| 15 | Nov. 19 Dec. 3.... | 88.49 | +24.16 | 1,298 | 4,500 | 32,321 | 2,590 | |
| 16 | Dec. 3 Dec. 17.... | 89.43 | +27.63 | 1,335 | 4,680 | 34,148 | 2,631 | |
| Steer B: | | | | | | | | |
| 1 | Dec. 27 to Jan. 10.... | 42.40 | −20.80 | 778 | 2,152 | [5]11,310 | 1,740 | |
| 2 | Jan. 10 Jan. 24.... | 34.17 | −21.67 | 590 | 1,354 | [5]7,100 | 1,736 | |
| 3 | Jan. 24 Feb. 7.... | 31.43 | −13.73 | 589 | 1,341 | 8,269 | 2,042 | |
| 4 | Feb. 7 Feb. 21.... | 30.98 | −12.08 | 592 | 1,357 | 8,383 | 2,045 | |
| 5 | Feb. 21 Mar. 6.... | 28.32 | −11.92 | 534 | 1,261 | 7,671 | 2,013 | |
| 6 | Mar. 6 Mar. 20.... | 27.94 | − 5.93 | 571 | 1,281 | 8,503 | 2,197 | |
| 7 | Mar. 20 Apr. 3.... | 25.60 | − 3.26 | 539 | 1,195 | 7,555 | 2,093 | 2,091 |
| 8 | Apr. 3 Apr. 17.... | 24.06 | − 7.50 | 473 | 1,195 | 7,478 | 2,071 | |
| 9 | Apr. 17 May 1.... | 26.54 | − 9.37 | 514 | 1,195 | 8,249 | 2,285 | |
| 10 | May 1 May 15.... | 22.79 | − 6.01 | 457 | 1,195 | 7,399 | 2,050 | |
| 11 | May 15 May 29.... | 24.48 | − 7.43 | 483 | 1,195 | 7,317 | 2,027 | |
| 12 | May 29 June 12.... | 23.91 | +26.53 | 915 | 2,618 | [5]18,415 | 2,328 | |
| 13 | Oct. 22 Nov. 5.... | 124.81 | +37.57 | 1,856 | 3,335 | 26,210 | 2,385 | |
| 14 | Nov. 5 Nov. 19.... | 201.91 | +68.31 | 3,059 | 3,858 | 34,371 | 2,491 | |
| 15 | Nov. 19 Dec. 3.... | 284.85 | +68.02 | 4,104 | 3,606 | 36,054 | 2,647 | |
| 16 | Dec. 3 Dec. 17.... | 308.43 | +20.35 | 4,047 | 3,521 | 32,823 | 2,470 | |

[1] See Table 2 for factors used to compute energy in hay and concentrates.

[2] See Table 28 for factors used to compute energy in feces in periods 1, 2, 3, 11, 13, and 16. In periods 4 to 10, inclusive, and period 12, for both steers the factor for energy in feces per gram of water-free substance was assumed to be 4.778 cals., based on the average of all heat determinations made on feces during hay feeding. In periods 14 and 15 the factors found in period 16 with steers A and B, respectively, were used.

[3] The energy in urine was computed by assuming for both steers 22 cals. per gram of urinary nitrogen (uncorrected for nitrogen equilibrium) for periods 1 to 11, inclusive, 30 cals. for period 12, and 12.63 cals. for periods 13 to 16, inclusive. (Based on data given by Armsby and Fries, U. S. Dept. Agric., Bureau Anim. Ind., Bull. 128, 1911; *ibid.*, Journ. Agric. Research, 1917, **11**, Table V, p. 454; also a personal communication from Professor W. W. Braman, of the Institute of Animal Nutrition.) The energy thus computed was corrected to nitrogen equilibrium by deducting 7.45 cals. for every gram of nitrogen lost from the body (Rubner, Zeitschr. f. Biol., 1885, **21**, pp. 316 and 329; *ibid.*, 1901, **42**, p. 303) or adding 7.45 cals. for every gram of nitrogen stored in the body.

[4] The energy in methane, periods 1 to 12, inclusive, was assumed to be 331 cals. per kilogram of water-free substance in hay (based on experiments with timothy hay reported by Armsby and Fries, Journ. Agric. Research, 1915, **3**, p. 441). In periods 13 to 16, inclusive, energy in methane computed from digestible carbohydrates in feed, assuming 4.5 grams methane per 100 grams digestible carbohydrates and 13.344 cals. per gram methane. (See Armsby and Fries, Journ. Agric. Research, 1915, **3**, p. 451; also, Armsby, Nutrition of farm animals, New York, 1917, p. 636.)

[5] See corrected values in Table 39, p. 165.

puted energy in urine and methane all entered into the final computations, the end-results of which are expressed in column *j* as the metabolizable energy per day. From the total metabolizable energy per day and the weight of feed, it is relatively simple to compute the metabolizable energy per kilo-

gram of water-free substance in the feed, a factor that has been frequently computed by other observers and found to be of considerable value. This computation is indicated in column *k* of Table 37.

The total metabolizable energy per day, as recorded in column *j*, shows that these animals were carried on an extraordinarily low level during periods 2 to 11, i. e., from January 10 to May 29. When the hay was increased in period 12 the metabolizable energy was more than doubled, and finally, with the fattening rations during periods 13 to 16, inclusive, the metabolizable energy was four and five times that during the submaintenance periods. While the variations in the total metabolizable energy per day are roughly proportional to the variations in the water-free substance in the feed per day, as is to be expected, particular interest lies in the metabolizable energy per kilogram of water-free substance in feed, as by this method of computation irregularities in amounts of feed from period to period are more nearly equalized. Rather wide variations are noted even on this basis of computation, the values ranging from as low as 1,627 calories in period 2 with steer A to as high as 2,647 calories in period 15 with steer B. Still, the large proportion of values range between 2,000 and 2,500 calories.

A long series of periods with both animals, periods 3 to 11, inclusive, give values fairly constant, but higher than those noted in periods 1 and 2. Since periods 2 to 11 represent submaintenance feeding exclusively with hay, the very low value found for available energy in period 2 with both steers, when essentially the same amount of feed was given as in the other submaintenance periods, might seem confusing, This low value, along with that found in period 1, is, however, readily explained by the irregularities in the feces excretion and variations in the amount of fill, which have been so frequently discussed in this report. Since period 3 was preceded by 14 days of constant feeding, we would expect uniformity in results thereafter until period 12, when the quantity of hay was more than doubled for 2 weeks.

It might at first sight appear that when two animals are given essentially the same amounts of water-free substance in feed for several months, the metabolizable energy per kilogram of water-free substance in feed per day would remain identical throughout this time. As a matter of fact, while the average values for periods 3 to 11, inclusive (see column *l*), for the two animals are very close to each other, the variations between individual periods are rather wide in the case of each animal. These animals were in the metabolism stalls the entire time. Most careful attention was paid to collection of urine and feces and weighing of feed. The tests with both animals were as nearly as possible in the nature of duplicate experiments. Under ordinary conditions a 2-week digestion experiment is presumed to be sufficiently long to give satisfactory results. It is quite obvious that the variations in the metabolizable energy per kilogram of water-free substance in feed in periods 3 to 11 are in large part to be accounted for by the rather wide differences in the amounts of feces excreted, and undoubtedly we have here to deal with the fact that even during 2-week periods with reduced amounts of feces due to curtailment of ration, the regularity in the expulsion of feces was not such as to secure an even distribution. If the digestion experiment with steer A had been made, for example, solely in period 5, i. e., from February 21 to March 6, the factor found, namely, 1,941 calories, would not

have been at all applicable to the next 2 weeks, when, as a matter of fact, the factor found was 2,276 calories.

Even if the factors for two periods are averaged, it is seen that while periods 10 and 11 with steer A average 2,128 calories, periods 6 and 7 average appreciably higher, 2,199 calories, while periods 4 and 5 average somewhat less. With the greatly decreased weights of feces, therefore, periods even of one month may hardly be said to be sufficient to determine accurately the relationship between feces and feed. It is true that the quantity of water-free substance in feed decreased slightly as time went on, but even making allowance for this, the records with both steers A and B show that a 2-week period is certainly not sufficiently long to establish a factor and in many instances a 4-week period will give erroneous results. The fact, however, that both animals, when studied over the entire period from January 24 to May 29, show average factors agreeing as closely as 2,131 calories with steer A and 2,091 calories with steer B is proof, we believe, that the grand average of these two average factors, namely, 2,111 calories, represents very closely the metabolizable energy per kilogram of water-free substance in hay, when the hay given is of the particular kind given steers A and B and the amount is as small as that given these animals.

Upon the resumption of maintenance feeding with hay alone in period 12, we have the same conditions obtaining as at the beginning of the experiment, namely, a marked changed in the amount of the ration, with undoubted disturbance in regularity of fecal excretion, and consequently the metabolizable energy per kilogram of water-free substance in feed immediately increases. We have no reason to believe that the irregularities in fecal excretion and variations in amount of fill do not completely explain this seeming discrepancy between the figures for period 12 and the preceding submaintenance periods. In estimating, therefore, the true metabolizable energy in hay, we have disregarded the values for periods 1, 2, and 12, and as the final grand average for both animals we find that the metabolizable energy in every kilogram of water-free substance in the hay amounted to 2,111 calories.

### METABOLIZABLE ENERGY IN PERIODS 1, 2, AND 12.

The proper computation of the metabolizable energy in the transition periods 1, 2, and 12, is important and warrants further treatment. When we consider that with both animals the feed was confined exclusively to hay in all the periods from 1 to 12, inclusive, and then examine the values for the metabolizable energy per kilogram of water-free substance in feed per day, as given in column $k$ of Table 37, we are immediately struck by the extraordinarily low figures for both animals in periods 1 and 2 and the high figures in period 12. Since these three periods all represent a hay ration, it would seem, *a priori*, as if the metabolizable energy per kilogram of water-free substance in feed would be more uniform, and that they would at least show the degree of uniformity noted in the submaintenance periods, 3 to 11, with each animal. In any estimate of the total probable needs of the organism on the different nutritive planes, and particularly as to how the quantity of feed met these needs, the most accurate computation of the metabolizable energy is necessary. In view of the important rôle that feces play in the estimation of metabolizable energy, the defect of too high a feed level in the

preliminary period prior to period 1, and the consequent transition in ration during period 2, grave doubt (as has already been pointed out) may be cast upon the low values for these first two periods with both animals and the question arises, What is the experience of other observers when feeding hay alone to animals on a maintenance ration?

Our data regarding submaintenance feeding in periods 3 to 11 may be said to be satisfactory, but for maintenance feeding periods 1 and 12 do not give

TABLE 38.—*Metabolizable energy in hay, as determined by Zuntz, Armsby, and Benedict and Ritzman. (Average values per day.)*

| Investigator and kind of hay used. | Steer, age, and weight. | Period of study. | Feed. (a) Water-free substance. | Feed. (b) Energy. | Energy in— (c) Feces. | Energy in— (d) Urine.[1] | Energy in— (e) Methane. |
|---|---|---|---|---|---|---|---|
| | | | *kg.* | *cal.* | *cal.* | *cal.* | *cal.* |
| Zuntz,[2] meadow hay. | Steer, 2½ yrs., 525 kg. | [3]I | 7.29 | 32,420 | 13,333 | 1,552 | 2,055 |
| Armsby,[4] timothy hay. | A, 3 yrs., 512 kg.... | [5]III | 2.97 | 13,412 | 5,475 | 606 | 1,096 |
| | | [3]IV | 4.89 | 22,116 | 9,237 | 975 | 1,747 |
| | B, 3 yrs., 379 kg... | [5]III | 2.80 | 12,618 | 5,247 | 627 | 1,057 |
| | | [3]IV | 4.63 | 20,930 | 8,879 | 965 | 1,641 |
| Benedict and Ritzman, mixed hay. | A, 3⅔ yrs., 522 kg. | [5]3 | 4.10 | 18,311 | 7,747 | 595 | 1,357 |
| | | [5]11 | 3.61 | 16,122 | 6,918 | 433 | 1,195 |
| | B, 3⅔ yrs., 495 kg. | [5]3 | 4.05 | 18,087 | 7,888 | 589 | 1,341 |
| | | [5]11 | 3.61 | 16,122 | 7,127 | 483 | 1,195 |

| Investigator and kind of hay used. | Steer, age, and weight. | Period of study. | Metabolizable energy per day. (f) Total. [b−(c+d+e)] | (g) Per kg. water-free substance in hay. (f÷a) | (h) Per kg. digestible organic matter. |
|---|---|---|---|---|---|
| | | | *cal.* | *cal.* | *cal.* |
| Zuntz,[2] meadow hay. | Steer, 2½ yrs., 525 kg. | [3]I | 15,480 | 2,123 | 3,647 |
| Armsby,[4] timothy hay. | A, 3 yrs., 512 kg.... | [5]III | 6,235 | 2,097 | 3,457 |
| | | [3]IV | 10,157 | 2,076 | 3,482 |
| | B, 3 yrs., 379 kg... | [5]III | 5,687 | 2,033 | 3,378 |
| | | [3]IV | 9,446 | 2,040 | 3,456 |
| Benedict and Ritzman, mixed hay. | A, 3⅔ yrs., 522 kg. | [5]3 | 8,612 | 2,100 | 3,618 |
| | | [5]11 | 7,576 | 2,099 | 3,642 |
| | B, 3⅔ yrs., 495 kg. | [5]3 | 8,269 | 2,042 | 3,549 |
| | | [5]11 | 7,317 | 2,027 | 3,604 |

[1] Energy in urine corrected for energy represented in nitrogen lost or stored in body.
[2] Von der Heide, Klein, and Zuntz, Landw. Jahrb., 1913, **44**, pp. 766, 769, 770, and 814.
[3] Maintenance ration.
[4] Armsby and Fries, U. S. Dept. Agric., Bureau Animal Industry, Bull. 128, 1911, pp. 25, 29. 164, 165, 168, 177, and 178. Experiments in 1907.
[5] Submaintenance ration.

concordant results and the experience of others must be relied upon to throw light on this matter. For this purpose we have collected in Table 38 certain data from the laboratories of Zuntz and Armsby, which are germane. Zuntz and his associates,[a] studying a 2½-year-old steer weighing 525 kg., which was fed exclusively meadow hay, found that the metabolizable energy per kilo-

[a] Von der Heide, Klein, and Zuntz, Landw. Jahrb., 1913, **44**, pp. 766, 769, 770, and 814.

gram of water-free substance in hay amounted to 2,123 calories. This value is essentially that found on the average for our two steers on the low-maintenance ration, a fact that justifies our belief that this value is not far from that which would normally be expected to be found with animals on a maintenance ration. Two of Armsby's animals,[a] one a 3-year old steer weighing 512 kg. and the other a 3-year old steer weighing 379 kg., were both fed timothy hay, period III representing a submaintenance ration and period IV a maintenance ration. The metabolizable energy per kilogram of water-free substance in hay, which ranged from 2,033 to 2,097 calories in these four periods with these two animals, is slightly lower than the result (2,123 calories) noted with the steer studied by Zuntz.

With our own animals it has already been pointed out that those periods less open to criticism are periods 3 to 11. Hence the computations for periods 3 and 11 only are included in Table 38. Unfortunately, the feces of steer A

TABLE 39.—*Metabolizable energy in feed; periods 1, 2, and 12.*

| Steer and period. | Water-free substance in feed per day. | Metabolizable energy per day. | |
|---|---|---|---|
| | | Uncorrected.[1] | Corrected.[2] |
| Steer A: | *kg.* | *cal.* | *cal.* |
| First period..... | 6.84 | 11,524 | 14,576 |
| Second period.... | 4.09 | 6,653 | 8,716 |
| Twelfth period.... | 7.91 | 18,953 | 16,856 |
| Steer B: | | | |
| First period..... | 6.50 | 11,310 | 13,592 |
| Second period.... | 4.09 | 7,100 | 8,552 |
| Twelfth period.... | 7.91 | 18,415 | 16,540 |

[1] See column *j*, Table 37, p. 161.

[2] Assumed for steer A, 2,131 cals. per kg. water-free substance in feed, and for steer B, 2,091 cals.

were lost for one day during period 3, so that the amount of feces excreted in this period is based on the average for 13 days, while the amount of feed eaten is based on the average for 14 days. It is hardly probable that this makes any appreciable error in the result. Turning immediately to the calculation of the metabolizable energy per kilogram of water-free substance in feed for our steers, we find values ranging from 2,027 calories to as high as 2,100 calories. While the results for steer A in periods 3 and 11, i. e., 2,100 and 2,099 calories, are both slightly below the general average for this animal, i. e., 2,131 calories, and the same is true of comparative values for steer B, nevertheless from an inspection of these figures it is evident that the grand average assumed by us of 2,111 calories, which is the average of 2,131 and 2,091 calories, with steers A and B, respectively, is not unlike that reported by Zuntz and by Armsby. Hence, although these two averages of 2,131 and 2,091 calories are based exclusively upon submaintenance periods, they may be and, indeed, should be, applied to the water-free substance in feed in periods 1 and 2 and, in all prob-

[a] Armsby and Fries, U. S. Dept. Agric., Bureau Animal Industry, Bull. 128, 1911, pp. 25, 29, 164, 165, 168, 177, 178.

ability, to that in period 12, to obtain the correct values for metabolizable energy. This correction, that is, assuming for steer A 2,131 calories and for steer B 2,091 calories per kilogram of water-free substance in feed, has been applied to periods 1, 2, and 12. The results are recorded in Table 39, p. 165. On this basis of computation it can be seen that the total metabolizable energy for period 1 with steer A is raised from 11,524 to 14,576 calories and with steer B from 11,310 to 13,592 calories. Similarly, in period 2, the total metabolizable energy with steer A is raised from 6,653 to 8,716 calories and with steer B from 7,100 to 8,552 calories. In period 12, when there was a sudden transition from submaintenance to maintenance feeding, the correction changes the original value of 18,953 calories to 16,856 calories in the case of steer A, and in the case of steer B from 18,415 to 16,540 calories. In any final use, therefore, of the metabolizable energy in periods 1, 2, and 12—that is, when a ration exclusively of hay was given—the corrected values for these periods should be employed rather than those based upon the original determinations, which, as previously stated, were profoundly affected by an error of technique in the case of period 1 and by the inevitable transition in ration necessitated by the plan of the experiment in periods 2 and 12.

### ALTERNATE METHOD FOR COMPUTING METABOLIZABLE ENERGY.

Based again upon standard factors derived chiefly from his classic researches, Armsby has found that the metabolizable energy is directly proportional to the digested organic matter and has proposed as a factor that for

TABLE 40.—*Metabolizable energy in feed, computed from digestible organic matter. (Average values per day.)*

| Steer and period. | Organic matter in water-free substance. | | | Metabolizable energy.[1] |
|---|---|---|---|---|
| | In hay. | In feces. | Digested. | |
| Steer A: | *kg.* | *kg.* | *kg.* | *cal.* |
| First period..... | 6.44 | 3.03 | 3.41 | 11,935 |
| Third period..... | 3.86 | 1.48 | 2.38 | 8,330 |
| Eleventh period.. | 3.40 | 1.32 | 2.08 | 7,280 |
| Steer B: | | | | |
| First period..... | 6.12 | 2.85 | 3.27 | 11,445 |
| Third period..... | 3.81 | 1.48 | 2.33 | 8,155 |
| Eleventh period.. | 3.40 | 1.37 | 2.03 | 7,105 |

[1] Assumed 3.5 calories per gram digestible organic matter (Armsby and Fries, Journ. Agric. Research, 1915, 3, p. 453).

each gram of digestible organic matter in the form of roughage, such as hay, there are 3.5 calories.[a] For concentrated feeds higher values are observed, depending upon the amount of digestible fat. As a control upon our method of computing the metabolizable energy, as outlined in detail in Table 37, we have also computed the metabolizable energy for periods 1, 3, and 11 by determining the amount of digested organic matter in each of these periods and multiplying this amount by Professor Armsby's factor of 3.5 calories. The

[a] Armsby and Fries, Journ. Agric. Research, 1915, 3, p. 453.

results are given in Table 40 and are directly comparable with the results given in column *j* of Table 37. This comparison shows that the metabolizable energy, as computed from the digested organic matter, is slightly higher in period 1 with both steers A and B, and in periods 3 and 11 a little lower with both animals. On the whole, the average agreement between the two methods of computation is very satisfactory. It is important to note, however, that the same errors that enter into the determination of the digestibility and the computation of the metabolizable energy in period 1 by the first method likewise obtain here, and the true picture of the total metabolizable energy in period 1 is more nearly expressed by the revised figures given in Table 39, based upon the average factors of 2,131 and 2,091 calories per kilogram of water-free substance in feed.

Since the metabolizable energy computed from the digested organic matter, as reported in Table 40, is lower in 4 out of 6 cases than the metabolizable energy computed from the energy in feed and excreta for the corresponding periods, it follows that conversely the metabolizable energy per gram of digested organic matter in feed (see Table 38, column *h*) will be somewhat larger with our animals than the general factor of 3.5 calories suggested by Armsby. It will immediately be noted, however, that the four values derived from his experiments of 1907 (indicated in Table 38) are all measurably lower than his factor of 3.5 calories. If from our own figures we attempt to deduce a factor representing the metabolizable energy per gram of digestible organic matter, we find that with steer A the factor is 3.618 calories in period 3 and 3.642 calories in period 11. With steer B it is 3.549 calories in period 3 and 3.604 calories in period 11. The metabolizable energy per gram of digestible organic matter in feed tends, therefore, to be slightly higher with our 2 animals on a submaintenance ration than the round figure of 3.5 calories suggested by Professor Armsby, and measurably higher than the average of the 4 experiments from his laboratory, given by us in Table 38 for comparison. The average of our 4 figures is 3.603 calories, a factor but 3 per cent higher than Armsby's round value of 3.5 calories. However, while this alternate method of computation serves as a most satisfactory check upon our original method of computation of the metabolizable energy, we feel strongly that the best method for determining the true metabolizable energy of our various animals on hay rations is to employ the average factor of 2,111 calories per kilogram of water-free substance in hay. For subsequent use, therefore, when a comparison is made between the metabolizable energy and the estimated heat-production of these animals, obviously the determined values, as given in column *j* of Table 37, will be used, except in the case of periods 1, 2, and 12, where the revised figures computed from the general factor 2,131 calories for steer A and 2,091 calories for steer B will be used. (See Table 39, p. 165.) In these three particular cases it seemed more logical to compute the metabolizable energy from the water-free substance in feed, using the individual average factor for each animal rather than the grand average for the two.

### Metabolizable Energy on Fattening Rations, Group IV.

Attention should be given to the fact that the total metabolizable energy is greatly increased during the fattening periods, 13 to 16 (an increase explained

wholly by the increase in feed), and likewise that the metabolizable energy per kilogram of water-free substance in feed, instead of being about 2,100 calories as found in hay periods, now rises with the admixture of concentrates in the feed to 2,500 and 2,600 calories or over. (See column *k*, Table 37.) This is in full conformity with the experience of Armsby and his associates[a] who found with concentrates high values, indeed at times much higher than we have noted.

The chief object of computing the factors representing the metabolizable energy per kilogram of water-free substance in feed per day in periods 13 to 16 with these two animals is to secure some data which may make it possible to compute the probable metabolizable energy in the case of steers 1 to 12, when on fattening rations. In other words, the general average factor of 2,111 calories can be used for animals 1 to 12, when on hay rations, but obviously a somewhat larger factor must be used for the fattening, concentrate rations. From the 8 different factors obtained with steers A and B in periods 13 to 16, an attempt has been made to select that factor which represents a ration as nearly as possible comparable with the ration employed in each individual case with steers 1 to 12, inclusive. An average of these 8 factors obtained with steers A and B can not be used, since the rations varied considerably in the amount of protein given the two animals. The factors for periods 13 to 16, therefore, have no special significance as applied to steers A and B, but are of practical value in computing the metabolizable energy with steers 1 to 12.

### Average Metabolizable Energy in Feed During the Main Feeding Periods, Group IV.

From the detailed computations given in Table 37 we have derived average values representing the total metabolizable energy in feed per day for steers

Table 41.—*Water-free substance and metabolizable energy in feed,*[1] *Group IV.* (*Average values per day.*)

| Period. | Date. | Steer A. | | Steer B. | |
|---|---|---|---|---|---|
| | | Water-free substance in feed. | Metabolizable energy. | Water-free substance in feed. | Metabolizable energy. |
| | 1919–20. | *kg.* | *cal.* | *kg.* | *cal.* |
| 1 | Dec. 27 to Jan. 10.... | 6.84 | 14,600 | 6.50 | 13,600 |
| 2 to 11 | Jan. 10 May 29.... | 3.79 | 8,100 | 3.80 | 7,900 |
| 12 | May 29 June 12.... | 7.91 | 16,900 | 7.91 | 16,500 |
| 13 | Oct. 22 Nov. 5.... | 11.00 | 23,300 | 10.99 | 26,200 |
| 14 to 16 | Nov. 5 Dec. 17.... | 13.08 | 33,800 | 13.57 | 34,400 |

[1] The blocks in Figs. 41 and 42, representing metabolizable energy in feed, are based on data in this table. (See Table 37, pp. 160 and 161, for detailed data.)

A and B while on maintenance, submaintenance, and fattening rations. These average values we have reported in Table 41, while in Figs. 41 and 42 (see pp. 297 and 298) we have represented the same data graphically in the

[a] Armsby and Fries, Journ. Agric. Research, 1915, 3, pp. 442 and 443.

form of blocks at the bottom of the charts. These directly determined data for steers A and B are practically all that are needed for the purpose of considering the energy balance and in how far the metabolizable energy suffices to meet the needs of these individual animals.

## Metabolizable Energy for Groups I, II, and III.

One of the most important functions of this series of observations with steers A and B was to secure, if possible, certain data regarding the digestibility and particularly the metabolizable energy of the feed, data which could properly be applied to animals 1 to 12 used in the preceding year, for with these animals no direct determinations of digestibility or metabolizable energy were made. As a result of our analysis of the values for metabolizable energy as actually determined with steers A and B, we believe that the best

Table 42.—*Water-free substance and metabolizable energy in feed. Group I.*
*(Average values per day.)*

[The blocks in Figs. 25, 26, and 27, representing metabolizable energy in feed, are based on data in this table.]

| Steer and date, 1918–19. | Water-free substance in feed. | Metabolizable energy. | Notes. |
|---|---|---|---|
| Steer 2: | *kg.* | *cal.* | For steer 2, since he received hay only through May 19, assumed 2,111 calories per kilogram water-free substance in feed for all dates. |
| Nov. 27 to Dec. 27 | 7.6 | 16,000 | |
| Dec. 28 Mar. 9 | 6.5 | 13,700 | |
| Mar. 10 May 19 | 6.9 | 14,600 | |
| Steer 4: | | | For steer 4 assumed 2,111 calories per kilogram water-free substance in feed for all dates through May 12; for May 13 to June 16, 2,491 calories, based on period 14 with steer B; for June 17 to July 14, 2,647 calories, based on period 15 with steer B; for July 15 to Aug. 27, 2,470 calories, based on period 16 with steer B. |
| Nov. 27 Dec. 27 | 8.7 | 18,400 | |
| Dec. 28 May 12 | 7.4 | 15,600 | |
| May 13 June 16 | 10.2 | 25,400 | |
| June 17 July 14 | 12.6 | 33,400 | |
| July 15 Aug. 27 | 15.0 | 37,100 | |
| Steer 5: | | | Steers 4 and 5 received both hay and grain from May 13 on; hay alone previous to May 13. |
| Nov. 27 Dec. 27 | 9.4 | 19,800 | |
| Dec. 28 May 5 | 8.3 | 17,500 | For steer 5 assumed 2,111 calories per kilogram water-free substance in feed for all dates through May 12; for May 13 to June 16, 2,532 calories, based on period 14 with steer A; for June 17 to July 14, 2,631 calories, based on period 16 with steer A; for July 15 to Aug. 27, 2,590 calories, based on period 15 with steer A. |
| May 6 May 12 | 10.5 | 22,200 | |
| May 13 June 16 | 11.2 | 28,400 | |
| June 17 July 14 | 14.3 | 37,600 | |
| July 15 Aug. 27 | 15.2 | 39,400 | |

factor to be used in computing the metabolizable energy in the case of steers 1 to 12 is the grand average of the two average values found with steers A and B in periods 3 to 11, namely, 2,111 calories per kilogram of water-free substance in hay. Certainly for those periods with steers 1 to 12 when hay alone was fed, namely, from November 27, 1918, to May 12, 1919, the use of this factor is perfectly justified.

During the fattening periods, with the mixed rations of hay and concentrates, the differences in the digestibility, in the urinary nitrogen, and in the processes of fermentation are such as to alter distinctly this factor of 2,111 calories, and direct averaging of the results obtained with steers A and B in

periods 13 to 16 is not justifiable, because of the difference in the protein content of the rations. Furthermore, the application of the factors secured with these two steers when on fattening rations to the case of steers 1 to 12 when on fattening rations is somewhat complicated, since the rations fed steers 1 to 12 for fattening were not identically in the same proportions as

TABLE 43.—*Water-free substance and metabolizable energy in feed. Group II. (Average values per day.)*

[The blocks in Figs. 30 to 34, representing metabolizable energy in feed, are based on data in this table.]

| Steer and date, 1918–19. | Water-free substance in feed. | Metabolizable energy. | Notes. |
|---|---|---|---|
| Steer 1: | *kg.* | *cal.* | |
| Nov. 27 to Dec. 21 | 9.3 | 19,600 | For steer 1 assumed 2,111 calories per kilogram water-free substance in feed for all dates through May 12; for May 13 to June 30, 2,561 calories, based on average of periods 14 and 15 with steer A; for July 1 to Oct. 27, 2,590 calories, based on period 15 with steer A; for Oct. 28 to Nov. 3, 2,561 calories, based on average of periods 14 and 15 with steer A. |
| Dec. 22 Dec. 27 | 4.9 | 10,300 | |
| Dec. 28 May 5 | 4.0 | 8,400 | |
| May 6 May 12 | 8.0 | 16,900 | |
| May 13 June 30 | 10.0 | 25,600 | |
| July 1 Oct. 27 | 14.4 | 37,300 | |
| Oct. 28 Nov. 3 | 6.8 | 17,400 | |
| Steer 3: | | | For steer 3 assumed 2,111 calories per kilogram water-free substance in feed for all dates through May 12; for May 13 to July 14, 2,569 calories, based on average of periods 14 and 15 with steer B; for July 15 to Oct. 27, 2,647 calories, based on period 15 with steer B; for Oct. 28 to Nov. 3, 2,647 calories, based on period 15 with steer B. |
| Nov. 27 Dec. 21 | 8.9 | 18,800 | |
| Dec. 22 Dec. 27 | 4.5 | 9,500 | |
| Dec. 28 May 5 | 3.7 | 7,800 | |
| May 6 May 12 | 8.8 | 18,600 | |
| May 13 July 14 | 11.5 | 29,500 | |
| July 15 Oct. 27 | 15.6 | 41,300 | |
| Oct. 28 Nov. 3 | 11.5 | 30,400 | |
| Steer 7: | | | For steer 7 assumed 2,111 calories for all dates through May 12; for May 13 to July 7, 2,561 calories, based on average of periods 14 and 15 with steer A; for July 8 to Nov. 3, 2,631 calories, based on period 16 with steer A. |
| Nov. 27 Dec. 21 | 7.1 | 15,000 | |
| Dec. 22 Dec. 27 | 3.9 | 8,200 | |
| Dec. 28 May 5 | 3.3 | 7,000 | |
| May 6 May 12 | 6.1 | 12,900 | |
| May 13 July 7 | 8.5 | 21,800 | |
| July 8 Nov. 3 | 12.4 | 32,600 | |
| Steer 10: | | | Steers 1, 3, 7, and 11 received hay and grain from May 13 on; hay alone previous to May 13. Steer 10 received hay and grain from July 8 on, and hay alone previous to July 8. For steer 10 assumed 2,111 calories per kilogram water-free substance in feed for all dates through July 7; for July 8 to Aug. 4, 2,491 calories, based on period 14 with steer B; for Aug. 5 to Nov. 3, 2,569 calories, based on average of periods 14 and 15 with steer B. |
| Nov. 27 Dec. 21 | 9.7 | 20,500 | |
| Dec. 22 Dec. 27 | 4.9 | 10,300 | |
| Dec. 28 May 5 | 4.1 | 8,700 | |
| May 6 May 12 | 5.6 | 11,800 | |
| May 13 July 7 | 7.5 | 15,800 | |
| July 8 Aug. 4 | 13.2 | 32,900 | |
| Aug. 5 Nov. 3 | 16.6 | 42,600 | |
| Steer 11: | | | For steer 11 assumed 2,111 calories per kilogram water-free substance in feed for all dates through May 12; for May 13 to June 23, 2,582 calories, based on average of periods 14 and 16 with steer A; for June 24 to Nov. 3, 2,590 calories, based on period 15 with steer A. |
| Nov. 27 Dec. 21 | 7.9 | 16,700 | |
| Dec. 22 Dec. 27 | 4.4 | 9,300 | |
| Dec. 28 May 5 | 3.3 | 7,000 | |
| May 6 May 12 | 6.5 | 13,700 | |
| May 13 June 23 | 9.6 | 24,800 | |
| June 24 Nov. 3 | 12.8 | 33,200 | |

those fed steers A and B. However, we believe that our selection of the correct factor to be used is such as to make the computations of the metabolizable energy for steers 1 to 12 even during the fattening periods reasonably accurate. The method of selection is perhaps, in all cases, somewhat ultra-refined and perhaps not justifiable, but the factors do represent, we believe, the closest estimate of the probable metabolizable energy per kilogram of

water-free substance in feed actually existing under the several conditions of rationing employed in the different periods.

The data for the metabolizable energy in the feed per day, as computed for Group I, i. e., the control steers, are given in Table 42. Of these animals, steer 2 was fed hay only until put on pasture on May 20, and hence the factor of 2,111 calories per kilogram of water-free substance in feed was used for all periods up to May 20. A typical instance of the use of the factors obtained with steers A and B on fattening rations can be seen in the case of steer 5. With this animal the factor for hay alone, namely, 2,111 calories, was used for all dates through May 12. From May 13 to June 16 the factor used

TABLE 44.—*Water-free substance and metabolizable energy in feed. Group III. (Average values per day.)*

[The blocks in Figs. 35 to 38, representing metabolizable energy in feed, are based on data in this table.]

| Steer and date, 1918–19. | Water-free substance in feed. | Metabolizable energy. | Notes. |
|---|---|---|---|
| Steer 6: | *kg.* | *cal.* | Steers 6 and 9 were on pasture from May 13 to Oct. 28, inclusive; during this time they also received hay from May 13 to 16, inclusive. They were taken off pasture Oct. 29, having been given hay since Oct. 5, in addition to pasturage; from Oct. 29 to Nov. 3, inclusive, they received both hay and grain, but no grass. Previous to May 13 they received hay alone. |
| Nov. 27 to Dec. 21 | 6.9 | 14,600 | |
| Dec. 22 Feb. 7 | 4.9 | 10,300 | |
| Feb. 8 May 5 | 2.8 | 5,900 | |
| May 6 May 12 | 6.4 | 13,500 | |
| Oct. 29 Nov. 3 | 9.7 | 23,100 | |
| Steer 8: | | | For steer 6 assumed 2,111 calories per kilogram water-free substance in feed for all dates through May 12; for Oct. 29 to Nov. 3, 2,385 calories, based on period 13 with steer B. |
| Nov. 27 Dec. 21 | 8.5 | 17,900 | |
| Dec. 22 Feb. 7 | 5.0 | 10,600 | |
| Feb. 8 May 5 | 2.9 | 6,100 | |
| May 6 May 12 | 6.5 | 13,700 | For steers 8 and 12, hay and grain from May 13 on; hay alone previous to May 13. |
| May 13 June 9 | 9.3 | 23,200 | |
| June 10 Sept. 1 | 13.7 | 33,800 | For steer 8 assumed 2,111 calories per kilogram water-free substance in feed for all dates through May 12; for May 13 to June 9, 2,491 calories, based on period 14 with steer B; for June 10 to Sept. 1, 2,470 calories, based on period 16 with steer B; for Sept. 2 to Nov. 3, 2,647 calories, based on period 15 with steer B. |
| Sept. 2 Nov. 3 | 12.6 | 33,400 | |
| Steer 9: | | | For steer 9 assumed 2,111 calories per kilogram water-free substance in feed for all dates through May 12; for Oct. 29 to Nov. 3, 2,122 calories, based on period 13 with steer A. |
| Nov. 27 Dec. 21 | 9.3 | 19,600 | |
| Dec. 22 Feb. 7 | 5.7 | 12,000 | |
| Feb. 8 May 5 | 3.8 | 8,000 | |
| May 6 May 12 | 8.1 | 17,100 | |
| Oct. 29 Nov. 3 | 11.4 | 24,200 | |
| Steer 12: | | | For steer 12 assumed 2,111 calories per kilogram water-free substance in feed for all dates through May 12; for May 13 to July 7, 2,569 calories, based on average of periods 14 and 15 with steer B; for July 8 to Nov. 3, 2,470 calories, based on period 16 with steer B. |
| Nov. 27 Dec. 21 | 7.2 | 15,200 | |
| Dec. 22 Feb. 7 | 4.2 | 8,900 | |
| Feb. 8 May 5 | 2.5 | 5,300 | |
| May 6 May 12 | 6.3 | 13,300 | |
| May 13 July 7 | 8.9 | 22,900 | |
| July 8 Nov. 3 | 11.5 | 28,400 | |

was 2,532 calories, based upon period 14 with steer A, a period in which the ration represented most closely, qualitatively and quantitatively, that given to steer 5 during this time. From June 17 to July 14 the factor was 2,631 calories, based upon the value for period 16 with steer A. From July 15 to August 27 the factor was 2,590 calories, based upon period 15 with steer A.

The values for metabolizable energy in feed for Group II are given in Table 43 and for Group III in Table 44. In these tables only the major subdivisions with considerable changes in ration are indicated. The notes in the several tables explain in each case exactly what factors were used for the computations.

Since in these tables the metabolizable energy in feed is computed directly from and hence is proportional to the water-free substance in feed, on this basis the data for the different animals are comparable. Where the feed is low in quantity the metabolizable energy is low. With steer 2 practically no change was made in the feed and the metabolizable energy remains essentially constant. With steer 4 the first two periods represent relative constancy on a maintenance hay ration, and the last three periods represent the refeeding and fattening rations. With steer 5 the first three periods are supposedly maintenance and the last three fattening. With Group II, subjected to a pronounced curtailment in ration, the first period with all 5 animals represents the supposed maintenance feeding with hay. This period is followed usually by two periods with curtailed ration, under which conditions the metabolizable energy is very much reduced. The period from May 6 to May 12 represents increased hay feeding with increased metabolizable energy, and finally, the later periods are fattening periods, save in the case of steer 10 which was fed a maintenance amount of hay only from May 13 to July 7.

With Group III the first period represents supposed maintenance, and the subsequent periods are based upon the two reductions in ration, the first taking place December 22 and the second February 8. Extraordinarily low figures are found during the period from February 8 to May 5. Steers 6 and 9 were put upon pasture after a very short period of feeding with increased hay alone, and no further data are available for them after May 12 until October 29, when they were brought back from pasture and fed hay and grain. Steers 8 and 12 were, however, given the usual fattening rations after May 12, with a corresponding increase in the metabolizable energy. The data for metabolizable energy, as given in Tables 42, 43, and 44, have been represented graphically in the form of blocks in Figs. 25 to 27 and 30 to 38, inclusive (see pp. 235 to 287).

## BODY MEASUREMENTS, GENERAL BODY CONDITIONS, AND PHYSIOLOGICAL FUNCTIONS.

Aside from the records of body-weight and its great alterations resulting from a reduction or addition in feed (which have already been discussed), a number of other measurements and observations were made which showed directly the influence of the submaintenance rations, and particularly the influence of the realimentation upon the physical and vital functions of these animals. Before discussing extensively the energy relationships and the energy balance, it seems advisable to point out the influence of these feeding levels as reflected in certain body measurements, body conditions, and physiological functions.

### Body Measurements.

A large series of measurements were taken throughout the entire period of experimentation with all the animals. A critical analysis of the general technique for taking body measurements and the difficulty of establishing exact landmarks (a difficulty which is not confined by any means to measurements on ruminants but applies likewise to humans) made it seem undesirable to present this mass of data with regard to body measurements. Information with regard to the effect of undernutrition upon the main dimensions

of the body is of course important, as it has a direct bearing, for example, upon the question as to whether or not with prolonged inanition the cartilage between the vertebræ is decreased. Our evidence, while perhaps suggestive, is not such as to justify any definite conclusions, and we do not feel warranted in publishing these data. Subsequent measurements upon animals with most carefully located landmarks, probably with the added verification of scale photography, can alone demonstrate this and other points.

Of the 9 different body measurements that we took periodically, trunk-length and height serve to give a fairly good picture of the general size of more or less mature animals, and may also be used to indicate increase in size during growth, but they are absolutely unreliable when obtained to indicate alterations in condition of flesh, and for this purpose chest circumference alone is in our judgment worthy of more than passing comment. Chest circumference is apparently accepted by many practical stockmen as the most reliable single index of the weight of steers and oxen. This measurement has been found to be a standard for estimating the live weight of cattle not only in New England but, indeed, among the Spanish-speaking people of the West Indies (in Porto Rico and Cuba), and perhaps it may have an even more extended application. In the studies carried out at the New Hampshire Agricultural Experiment Station on the inheritance of body contour and its relation to body conformation in sheep,[a] it has been found that any material variation in the circumference of the chest in the same mature individual is due mainly to variation in the condition of fleshiness, provided the measuring chain is applied as far forward as the elbows or forelegs of the animal permit. This particular location is not subject to temporary, transitory fluctuations due to alterations in the contents of the alimentary tract, for measurements on steers taken immediately before and after watering have not shown any significant differences due to increased fill, even after the consumption of relatively large volumes of water. Fill due to feed also seems to affect the chest circumference but very little at a point immediately behind the forelegs. In fact, if ingestion of feed or water caused any perceptible pressure on the organs within the thoracic cavity, it would probably interfere with their normal functioning. Of course, as the distance increases posteriorly from the foreleg, the effect of fill on the body circumference due especially to the expansion of the paunch or rumen becomes more marked, reaching its maximum somewhat forward of the hips.

We have recorded in Table 45 the circumferences of our steers 1 to 12, measured in the most forward position, i. e., immediately behind the forelegs. These measurements (which unfortunately include only one taken prior to the ration curtailment, namely, that of December 20, 1918) consist for the most part of a series taken immediately after refeeding began, and show very clearly the influence of the 180 days of increased heavy feeding, a period which in length of time also represents the normal fattening period for steers in the corn-belt region. A rough comparison of the body-weight curves of these animals, which we have already considered, and the general trend of the increases in circumferences, as indicated in Table 45, shows that the

[a] Ritzman and Davenport, New Hampshire College, Agric. Expt. Sta., Tech. Bull. No. 15, April, 1920.

chest circumference forms a fairly reliable, general index of the storage of flesh and fat.

Until June 17, or during the first 5 weeks, only two or three daily measurements were taken in each weekly period. After that date the measurements were taken daily, and with three exceptions the averages represent seven measurements. The measurements on December 20, 1918, were taken when the animals were in a normal condition of flesh, soon after they were purchased, and somewhat over a month after they had come off pasture, during which time they had been fed a liberal supply of native hay, i. e., sufficient hay to hold their weight approximately. Those on May 11 and 12 were made after

TABLE 45.—*Measurements of chest circumference. Groups I, II, and III.* (*Average values.*)

| Date. | Group I. | | | Group II. | | | | | Group III. | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Steer 2. | Steer 4. | Steer 5. | Steer 1. | Steer 3. | Steer 7. | Steer 10. | Steer 11. | Steer 6. | Steer 8. | Steer 9. | Steer 12. |
| 1918–19. | cm. | cm. | cm. | cm. | cm. | cm. | cm. | cm. | cm. | cm. | cm. | cm. |
| Dec. 20 | 180 | 189 | 199 | 199 | 188 | 185 | 194 | 190 | 179 | 182 | 204 | 180 |
| May 11 to May 12 | 176 | 189 | 197 | 184 | 182 | 174 | 186 | 181 | 174 | 170 | 196 | 170 |
| May 13 May 19 | 177 | 187 | 197 | 186 | 179 | 173 | 185 | 180 | 170 | 169 | 194 | 170 |
| May 20 May 26 | ..... | 189 | 196 | 187 | 182 | 173 | 186 | 180 | 173 | 172 | 196 | 173 |
| May 27 June 2 | ..... | 189 | 194 | 186 | 182 | 174 | 185 | 182 | 173 | 171 | 194 | 173 |
| June 3 June 9 | ..... | 191 | 194 | 184 | 181 | 173 | 183 | 183 | 176 | 171 | 198 | 171 |
| June 10 June 16 | ..... | 191 | 197 | 186 | 183 | 175 | 187 | 182 | 175 | 174 | 199 | 175 |
| June 17 June 23 | ..... | 191 | 198 | 187 | 185 | 175 | 183 | 181 | 176 | 174 | 198 | 173 |
| June 24 June 30 | ..... | 194 | 200 | 189 | 187 | 177 | 184 | 184 | 177 | 180 | 201 | 176 |
| July 1 July 7 | ..... | 194 | 203 | 190 | 187 | 179 | 184 | 185 | 178 | 180 | 201 | 177 |
| July 8 July 14 | ..... | 197 | 204 | 193 | 190 | 179 | 186 | 186 | 179 | 181 | 203 | 179 |
| July 15 July 21 | 183 | 198 | 206 | 195 | 190 | 182 | 188 | 188 | 182 | 183 | 203 | 181 |
| July 22 July 28 | 183 | 198 | 207 | 198 | 191 | 184 | 187 | 189 | 182 | 186 | 204 | 182 |
| July 29 Aug. 4 | 184 | 200 | 209 | 201 | 194 | 186 | 192 | 194 | 183 | 188 | 206 | 184 |
| Aug. 5 Aug. 11 | 185 | 202 | 212 | 203 | 195 | 188 | 192 | 196 | 185 | 190 | 208 | 187 |
| Aug. 12 Aug. 18 | 185 | 202 | 213 | 203 | 197 | 190 | 192 | 197 | 185 | 192 | 208 | 188 |
| Aug. 19 Aug. 25 | 185 | 203 | 213 | 204 | 197 | 191 | 195 | 198 | 183 | 195 | 207 | 190 |
| Aug. 26 Sept. 1 | 184 | 205 | 213 | 204 | 198 | 194 | 196 | 198 | 186 | 194 | 208 | 192 |
| Sept. 2 Sept. 8 | ..... | ..... | ..... | 206 | 199 | 193 | 198 | 199 | 186 | 196 | 208 | 195 |
| Sept. 9 Sept. 15 | ..... | ..... | ..... | 206 | 199 | 194 | 198 | 199 | 183 | 196 | 207 | 195 |
| Sept. 16 Sept. 22 | ..... | ..... | ..... | 207 | 200 | 196 | 200 | 202 | 183 | 197 | 207 | 194 |
| Sept. 23 Sept. 29 | ..... | ..... | ..... | 208 | 201 | 198 | 202 | 202 | 184 | 198 | 206 | 194 |
| Sept. 30 Oct. 6 | ..... | ..... | ..... | 209 | 203 | 200 | 205 | 205 | 184 | 199 | 207 | 196 |
| Oct. 7 Oct. 13 | ..... | ..... | ..... | 211 | 205 | 201 | 207 | 207 | 185 | 201 | 208 | 197 |
| Oct. 14 Oct. 20 | ..... | ..... | ..... | 211 | 205 | 201 | 207 | 207 | 186 | 199 | 206 | 199 |
| Oct. 21 Oct. 27 | ..... | ..... | ..... | 213 | 207 | 201 | 207 | 208 | 185 | 198 | 208 | 199 |
| Oct. 28 Nov. 3 | ..... | ..... | ..... | 212 | 207 | 201 | 210 | 207 | 186 | 200 | 208 | 199 |

the steers had been carried for 135 days on submaintenance rations (except for the control animals) and had again been on an assumed maintenance ration of hay alone for one week. The measurements of May 11 and 12, therefore, could not represent any material increase in tissue, although they might represent a fairly normal condition of fill, as the amount of hay given at this time was subsequently increased but very little during the fattening period, the added ration being almost entirely concentrates. After May 12, steers 2, 6, and 9 were on pasture; No. 10 received the supposedly maintenance amount of hay given him at the beginning of the experiment until July 8, when he was put on a ration of hay and grain; and Nos. 1, 3, 4, 5, 7, 8, 11, and 12 were put on low grain rations in addition to the hay, the quantity of grain being gradually increased.

A pronounced decrease in chest circumference is noted between December 20 and May 11 with all the animals except Nos. 2, 4, and 5, the control group. Of these, No 4 shows no change and Nos. 2 and 5 show a decrease of 4 and 2 cm., respectively. The fact that steers 2 and 5 show a change of 2 to 4 cm., and that steer 6 could be subjected for so long a period of submaintenance and show a change of only 5 cm. is indeed surprising. All the other animals show very material alterations, amounting usually to over 8 cm., and in the case of steer 1 to as high as 15 cm. Of special significance is the fact that after May 11 to 12 this chest measurement remains for several weeks, at least until about June 3, at a fairly constant value with each of the animals in the submaintenance groups, although during this time they were being given extra feed, and undoubtedly there was a large accumulation of fill. This bears out again our contention that changes in fill have very little, if any, effect upon the chest measurement, as outlined. After June 3 there is practically a constant increase in the measurement until the end of the fattening period, the striking exceptions to this being Nos. 2, 6, and 9. With steer 9 a maximum of 208 cm. was reached on August 5 and held throughout the rest of the year and with steer 6 there were also very slight changes after this date, but it is to be recalled that these two animals were upon pasture. With steer 2 there was a rapid increase between May 13 and July 15, when he was brought off pasture for measurement, but thereafter the chest circumference remained constant.

With steers A and B the chest circumferences were measured only at three different times, i. e., on June 5, November 5, and December 21, 1920. The records, in centimeters, are as follows:

| | June 5. | Nov. 5. | Dec. 21. |
|---|---|---|---|
| Steer A..... | 185 | 200 | 210 |
| Steer B..... | 179 | 195 | 200 |

Unfortunately, no measurements were taken at the beginning of the curtailment of ration, but in our judgment, on November 5, 1920, when the second measurements were made, the steers were in about the same condition of flesh as they were at the beginning of the feed cut. On the other hand, when the first measurements were recorded with these animals on June 5, 1920, they were just at the end of their long period of submaintenance. Under the circumstances we can only assume that the November figures correspond to those prior to the ration curtailment, and that as a result of the curtailment there was a loss of 15 cm. in the case of steer A and 16 cm. in the case of steer B. The influence of the heavy fattening rations during the period from November 5 to December 21 is immediately reflected in the increased chest circumferences. Again these two animals bear out the general conclusions drawn from steers 1 to 12.

One important use of these chest circumferences is the light that they throw upon the unsettled question of the amount and influence of changes in fill. Although with steers A and B measurements were taken only at the chest and not at the paunch and flank, subsequent to these observations a series of

fasting experiments were made with steers, when of course there was a very great loss of fill. The effect of the loss in fill due to fasting is most noticeable in the paunch and hind flank. Fasting periods of 7 to 14 days caused a marked decrease in the circumference of the hind flank, a slightly smaller decrease in that of the paunch, and only a relatively negligible decrease in the circumference of the chest just behind the foreleg. With two adult animals the relative shrinkages, expressed in percentages of the original measurements taken with the animals with complete fill, were as follows: chest, 3.8 per cent; paunch, 12 per cent; hind flank, 13.5 per cent. So far as visual comparisons are concerned between animals carried on submaintenance rations for a very extended period and animals which have fasted for short periods of 7 to 14 days, it would seem that the judgments of general appearance are very similar.

The fact that on refeeding our animals only slowly began to show an increase in the chest circumference measured behind the foreleg, although at the same time their increase in weight was relatively enormous, is further evidence that the change in weight at first was in large part due to fill and not to the deposition of organized body-tissue. We regret extremely that the paunch and flank circumferences were not measured during this stage of feeding. In the fasting experiments in progress at the moment of writing very complete data are being secured.

### Observations on General Behavior.

The effect of a sudden reduction in feed to a point materially below weight maintenance had a pronounced effect on the normal activities of certain of the animals. Strictly speaking, perhaps these curtailments should have been made under such conditions that the animals would not see other animals having the normal amount of feed during time of feeding. Usually there was greatly increased nervousness or uneasiness, although there was a difference between individuals in the degree to which they showed these symptoms. For example, Nos. 1, 7, and 10 were much more irritable than the others, while steers A and B showed irritable symptoms to a less extent than the steers of Groups I, II, and III. This may possibly be explained by the fact that steers A and B were in darker quarters and living under greater restrictions as to movement and exercise, although there was undoubtedly some difference due to greater inherited nervousness or docility. The general restlessness and craving for feed subsided after a week or ten days.

In connection with the general restlessness, it seemed to us as if the demand for mere bulk or fill was as much the cause of craving for feed as the demand for digestible or metabolizable material, in fact, perhaps more so, since all the animals showed an apparently apathetic attitude to the conditions of the experiment after the digestive tract had once become adjusted to the quantitative change in contents. As a matter of fact, it was observed that after this adjustment took place the control animals, Nos. 2, 4, and 5, showed much more eagerness and concern to get their portion at feeding-time than did the animals on curtailed rations, and likewise showed by contrast with the underfed animals a more nervous disposition. In a similar manner a subsidiary experiment carried out on some Hereford steers confirmed our obser-

vation that the animals craved bulk. In the early part of February, 1919, we placed a smaller group of Herefords in a small barn and conducted a practical check on our main feeding experiments as follows. The animals were divided into two lots with the object of carrying them through the winter on native hay, with a supplement of cottonseed meal and bran mixture to bring the ration to the maintenance requirement. Four steers received a full ration for maintenance, and with these steers there was reasonable growth, but no change in flesh. Three steers were given one-half their usual ration, and it was observed that when these steers were given grain first and then hay, they would leave the grain to eat the hay, apparently craving bulk. At the beginning of the experiment, when the steers on the submaintenance ration were given grain first and hay only after they had cleaned up the grain, scouring would result, but when given hay first and grain afterwards, there would be no scouring. Whenever the animals were given an option, they would invariably leave the grain to eat the hay.

A certain control as regards the relative activity in the stall was possible from superficial observation as to the number of times the animals were found lying down and as to the alertness they showed in rising to their feet. With regard to this last point, it was observed that the control steers were the first to rise to their feet when the attendants came into the barn, and Group II were the last to rise. Singularly enough, the records, sparse though they are, show that the control animals were found lying down a larger number of times than were the submaintenance animals. The reduction in the amount of feed also had a marked effect on the frequency of rumination, the animals with the lowest amounts of feed ruminating very little.[a] Steer 11 at times showed an unusual behavior in ruminating just prior to being led to the respiration chamber when he had been deprived of feed for 24 hours, although no such delayed action was observed in any of the other steers. On the whole, all of the steers were more persistent in lying down right after the feed was consumed during the fattening period than in the submaintenance period, which may be due to the fact that cattle seem to ruminate more commonly when lying and that submaintenance animals have less occasion to ruminate.

As steers 1 to 12 were turned out into a yard for exercise almost daily, their general behavior could be observed under more varying conditions of normalcy and lack of restraint than in the case of steers A and B. During this exercise period some differences in behavior were observed, although these were not entirely proportional to the amounts of feed. In general, the animals on submaintenance rations moved around more slowly and with less vigor than the control animals, but apparently showed a desire for exercise. Nos. 1 and 11 showed, on the whole, more activity in this respect than the other animals on curtailed rations, and in fact these two individuals showed at times a strong sexual tendency, even to the end of the submaintenance period.

[a] Rumination is apparently a provision for the preparation of roughage only, since Henry and Morrison (Feeds and feeding, Madison, Wisconsin, 1916, 16th ed., p. 72) cite evidence that rumination ceases when coarse food is withdrawn from a ration and only concentrates are fed.

### The Effect of Submaintenance Rations on General Condition.

The first noticeable effect of the reduction of feed on the general condition of the animals was observed in a shrinking of the paunch, due of course to a change in the fill of both feed and water.[a] The result of this shrinkage gave the animals a more rangy appearance, although there was no impression of emaciation until well along in the experiment, when they began to shrink up in the flanks and to lose the covering over the ribs, along the spine, and in the thighs. The submaintenance ration also reacted on the condition of the hair and skin. A lack of luster in the hair became manifest after about a month of undernutrition, and the skin became drier and began to adhere more closely. These conditions became more marked after the middle of the period of undernutrition, and toward the end the skin became exceedingly dry and tight, showing a tendency to crack and become scaly, a lot of dead tissue peeling off around the rump. At this point there was also some shedding of hair, and the animals showed symptoms of irritation of the skin in their desire to rub. In the case of steers 1 to 12 this irritation was very much accentuated by a temporary infestation of lice which occurred during the early part of March 1919, and which was particularly severe with the animals on submaintenance rations. However, the steers were immediately treated and cured. There was some difference between individuals in the degree of shedding of hair, Nos. 7, 8, 9, and 11, which were most heavily infested with lice, shedding the hair in patches. Steers A and B also shed quantities of hair during the last half of the submaintenance period,[b] so that their coats looked fairly thin, as did those of the 12 steers of the preceding year at the close of undernutrition.[c]

On the night of March 16, No. 8 caught his foot in the chain tie-up, which caused a temporary swelling of the leg and a rise in pulse for that day, although by the following day the swelling subsided (after treatment) and the pulse was back to normal. During February, No. 2, one of the control animals, developed a hard lump about the size of a hen's egg on the jaw, which lasted until August 23, when it broke just before the animal was slaughtered. During this time he showed no particular signs of discomfort or illness, and his temperature was normal during this whole period.

It is a common practice of live-stock experts to score animals at different stages of their development, and these scores may properly be used as indications of the differences in condition of the animal at various times of the year. Without publishing in detail the results of the scoring of these animals, reference may be made here simply to Table 59 (p. 223). In this table the animals are scored upon the basis of whether they were fat (F), medium (M), thin (T),

[a] In the case of steers A and B, for which an exact record of water consumption was kept, the lessened water consumption, which was proportional to the percentage reduction in feed, became effective at once when the feed was reduced.

[b] As early as March 2 it was observed that the skin became much drier, adhering to the body and showing an apparent tendency to crack, hair sloughing off in spots. By March 20 these symptoms had become more accentuated and were recorded as one of the more noticeable effects of submaintenance.

[c] It is a characteristic of all cattle to shed their coats of hair during the spring, the winter coats being largely replaced by new growth, so that with our steers the failure to replace the loss of hair due to lack of proper nourishment of the skin rather than actual loss itself may have been the more pronounced result, although the shedding was no doubt hastened and accentuated by lack of nourishment.

or emaciated (E), a plus or minus scale being allowed under each gross head. All except the three control animals were in an emaciated condition on May 5 at the end of the submaintenance period, and of these Nos. 1, 6, 8, 9, and 12 showed a score of E−, or the lowest condition of all. Just prior to slaughter, the control animals, Nos. 4 and 5, were scored as F− and No. 2 as M+ (and it will be recalled that No. 2 was the grass-fed animal of this group). The animals in Group II were all scored on November 3 as F−, while of the animals in Group III No. 6 was T+, No. 8 was F+, No. 9 was E+, and No. 12 was M−. Steers A and B were given exactly the same scoring on all dates, for on January 2, 1920, they were M−, on May 29, E+, and on December 26, M+. It will be observed in general that these relative scorings conform quite closely to the changes in growth measurements noted at the chest. Further consideration of the scoring of these animals, particularly the scoring just before slaughter, is deferred until a subsequent section.

### Rectal Temperature.

Since, in this investigation, it was proposed to curtail markedly the rations of certain of our animals, we felt as if body-temperature measurements had at least a comparative value, not only between the two submaintenance groups and the control group, but between the different groups at different seasons of the year. Consequently we consider the data worth publishing in abstract, although recognizing clearly that the investigation as a whole is subject to the general criticism raised by Kriss[a] that temperature measurements should be taken deeper in the rectum or vagina than they commonly are. But since the technique was uniform in all instances, we believe that for comparative purposes the results are reliable. Furthermore, the technique employed was that commonly used by all veterinarians for determining the rectal temperatures of cattle.

The profound influence of the curtailment of ration upon the general bodily functions makes it necessary for us to examine critically the rectal temperatures taken throughout the entire series. With steers 1 to 12 many hundreds of temperature measurements were taken. Indeed, they began with all the animals on December 15, and with each steer we have 4 normal measurements between December 15 and 21 before any alteration in ration was made. In Table 46 are recorded the average rectal temperatures for the several animals in Groups I, II, and III in typical periods throughout the year, representing distinct nutritive levels. These averages are based on 4 to 7 measurements in each case.

Considering, first, the average normal values secured from December 15 to 21, while the steers were on maintenance rations, we find that the average rectal temperature for 4 days ranges from a minimum of 101.0° F. with steers 2 and 10 to a maximum of 101.9° F. with steers 6 and 8. The average for all 12 steers, representing 48 different measurements, is 101.5° F. The variations in the average temperatures noted in the maintenance period amount to essentially 1° F. Disregarding for the moment the fact that these animals were not treated exactly alike, i. e., disregarding the fact that Nos. 2, 4, and 5 were fed on maintenance, we note for the period from January 16 to 30 a

[a] Kriss, Journ. Agric. Research, 1921, 21, p. 1.

minimum temperature of 101.1° F. with steer 10 and a maximum temperature of 102.0° F. with steers 4 and 9. Here the variation between the extremes is 0.9° F., essentially that noted at the normal feed-level, but the temperatures are on the whole slightly higher at this period. When we consider the data during the period from March 1 to 14, we find the range here is from 101.2° F. with steer 1 to 102.2° F. with steers 4 and 6, a range identical with that noted at the earlier stages, steer 4 showing absolutely the highest value in both the second and third periods. In the period from April 2 to 16, inclusive, the temperature ranges from 100.2° F. with steer 5 to 101.6° F. with steer 4. In July during the period of full feeding, the temperatures were measured for 4 days with all the animals except steer 2, who was measured on but 1 day. With steer 2 the measurement was 101.4° F. With the other animals the temperature ranged from 100.9° F. with Nos. 3, 7, 10, 11, 8, and 12, to 101.5° F. with steer 5.

TABLE 46.—*Average rectal temperatures at typical periods throughout the year. Groups I, II, and III.*

| Group and Steer No. | Dec. 15 to 21.[1] | Jan. 16 to 30.[2] | Mar. 1 to 14.[2] | Apr. 2 to 16.[2] | July 1 to 25.[3] |
|---|---|---|---|---|---|
| Group I: | °F. | °F. | °F. | °F. | °F. |
| Steer No. 2 | 101.0 | 101.9 | 101.9 | 101.5 | [4]101.4 |
| Steer No. 4 | 101.5 | 102.0 | 102.2 | 101.6 | 101.4 |
| Steer No. 5 | 101.5 | 101.3 | 101.5 | 100.2 | 101.5 |
| Group II: | | | | | |
| Steer No. 1 | 101.4 | 101.8 | 101.2 | 100.9 | 101.2 |
| Steer No. 3 | 101.4 | 101.8 | 101.9 | 101.0 | 100.9 |
| Steer No. 7 | 101.5 | 101.6 | 101.4 | 100.9 | 100.9 |
| Steer No. 10 | 101.0 | 101.1 | 101.7 | 100.9 | 100.9 |
| Steer No. 11 | 101.5 | 101.8 | 102.1 | 101.3 | 100.9 |
| Group III: | | | | | |
| Steer No. 6 | 101.9 | 101.6 | 102.2 | 101.4 | 101.4 |
| Steer No. 8 | 101.9 | 101.8 | 101.9 | 101.2 | 100.9 |
| Steer No. 9 | 101.6 | 102.0 | 101.7 | 101.3 | 101.4 |
| Steer No. 12 | 101.7 | 101.6 | 101.4 | 100.7 | 100.9 |

[1] Maintenance period with all groups.
[2] Jan. 16 to Apr. 16, submaintenance period with Groups II and III; maintenance period with Group I.
[3] Fattening period with all groups; steers 2, 6, and 9 on pasture.
[4] Represents a single record and not an average.

While the foregoing treatment of temperatures shows rather narrow ranges, and that the range is not widened perceptibly when certain of the animals are on reduced ration, even when the control animals are compared with them, a further consideration is desirable of the temperature ranges with the special groups, II and III. With the animals of Group II, which were subjected to a great curtailment in ration and whose metabolism finally reached a very low level, we find that the rectal temperature for the submaintenance level during a period of approximately 3 months, i. e., from January 16 to April 16, was 101.3° F. with steer 1, while the initial normal value for the 4 days in December was 101.4° F.; with steer 3 it was 101.6° F., as compared to the normal value of 101.4° F.; with steer 7 it was 101.3° F., as compared to 101.5° F.; with steer 10, 101.2° F., as compared to 101.0° F.;

with steer 11, 101.7° F., as compared to 101.5° F. In Group II, therefore, 3 of the 5 animals show slightly higher temperatures during the submaintenance period and 2 show temperatures 0.1 and 0.2° F. lower. With Group III, during the lowest feed-level, from February 8 to May 5, the average rectal temperature, according to Table 46, with steer 6 was 101.8° F. as against a normal temperature of 101.9° F.; with steer 8, 101.6° F. as against 101.9° F.; with steer 9, 101.5° F. as against 101.6° F.; and with steer 12, 101.1° F. as against 101.7 °F. In this group all the animals show a slightly lower temperature at the low feed-level. The data for both groups, when considered collectively, however, give no clear evidence that undernutrition has any effect upon the rectal temperature, as measured by us.

From our general impression of the course of the rectal-temperature measurements obtained in the first year's work, it was decided that with steers A and B the observations could be less extensive. The result was that during the entire year there were only 14 days when temperature measurements were made with each animal. The first observation was on January 21, 1920, and the last on December 16, 1920. The range in rectal temperature with steer A was but from 100.7° F. on May 2 to 102.5° F. on January 21, and with steer B from 99.8° F. on May 7 to 103.8° F. on December 16. In this latter case the variation amounted to 4° F. There is nothing in the protocols to explain this wide variation. The high temperature of 103.8° F. is not coincidental with the highest metabolism value with steer B. In the light of our experience with the 12 other steers, it seems highly improbable that the variation found with steer B has any connection whatsoever with the alteration in ration.

With the tremendous alteration in the metabolic level, when the whole organism was subsisting on a very greatly reduced nutritive plane and the heart beating at a very much reduced rate, it is perhaps somewhat surprising that there should have been practically no change in the rectal temperature. With humans some correlation between rectal temperature and metabolism, particularly in conditions of disease, is to be noted. Indeed, Du Bois[a] has recently contended that the human body obeys van't Hoff's law with wonderful exactness.

### Skin Temperature.

The sensitivity to cold noted with groups of young men placed upon low diets[b] and the fact that certain of our animals on submaintenance seemed to be especially prone to shiver, led us to make a series of skin-temperature measurements of these animals on the last day of submaintenance, May 5. Eleven animals in Groups I, II, and III, including the control animals, were measured at 6 different positions on the skin. The twelfth animal, steer 1, was inside the respiration apparatus in another building on this particular date, and hence no measurements were secured with him. The outline drawing of a steer in Fig. 24 shows in the numbered positions the approximate locations at which the skin temperature was measured on each of the 11 animals. These measurements were taken on the outside of the hair and not at the base of the hair.

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[a] Du Bois, Journ. Am. Med. Assoc., 1921, 77, p. 354.
[b] Benedict, Miles, Roth, and Smith, Carnegie Inst. Wash. Pub. No. 280, 1919, p. 255.

Unfortunately, the barn temperature was not recorded at the time these temperatures were taken, other than the regular graphic tracing on the automatic recording apparatus, which unfortunately was some distance from the exact place at which our temperature measurements were made. It is worthy of note, however, that our graphic records do show an unusually high temperature at noon of the day when these measurements were made, and they were all made between $11^h\ 45^m$ a. m. and $1^h\ 15^m$ p. m. Although a high temperature of 34° C. was indicated on the recording thermometer at about this time, we can place but little reliance upon this for actual comparison with the skin temperatures of our animals, other than as indicating that the barn was probably somewhat warmer than usual.

Our main concern at this time, however, was a comparison of the skin temperatures of the control animals and those which had been subjected to a curtailment of ration. The data are recorded in Table 47 herewith for each ani-

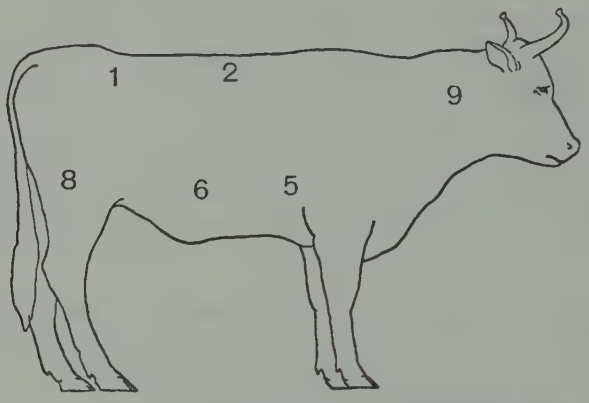


FIG. 24.—Outline drawing of a steer, showing the numbered locations of the skin-temperature measurements.

mal at each individual position. Although a study of the skin temperature *per se* was not our main object, it is of interest to notice how the temperatures varied at the different positions with the individual animals. This point is perhaps best shown in the averages at the foot of the table, where it is seen that the lowest average skin temperature is that in position 2, namely, 32.5° C., and the highest that in position 9, namely, 33.4° C., the extreme range therefore being but 0.9° C. This is in striking contrast to the series of skin-temperature measurements made with a large number of hairless animals at the New York Zoological Park,[a] animals that had been exposed for many hours to a temperature of 19.5° C. On these animals very much wider differences were observed. It is to be noted, however, that in the latter case we are dealing with hairless animals.

Referring to the differences in skin-temperature measurements between the different animals, we must recall that steers 2, 4, and 5 were normal, and it is the temperatures of these animals that we are to compare with those of the others. The average values given in the last column of Table 47 show that

[a] Benedict, Fox, and Baker, Am. Journ. Physiol., 1921, 56, p. 464; *ibid.*, Proc. Nat. Acad. Sci., 1921, 7, p. 154.

the highest average skin temperature on any animal, 33.7° C., was noted with steer 5. The next highest temperature, 33.6° C., was noted with steer 2. Both of them were control animals. Steer 8 also had an average temperature of 33.6° C. but, on the other hand, steer 4, another of the control animals, had an average temperature of 33.0° C. There is, therefore, a distinct tendency for the 3 control animals on the whole to have skin temperatures somewhat higher than the general average for all 11 animals of 32.8° C.

Our measurements are not extensive enough for us to be able to note the influence of environmental temperature, which must be great, but, as already pointed out, this whole investigation of skin temperatures was made on the comparative or relative basis. The omission of a suitable, careful record of the environmental temperature from this series of measurements is serious,

TABLE 47.—*Skin temperatures. Groups I, II, and III. May 5, 1919.*

| Group and Steer No. | Position of measurement.[1] | | | | | | Average skin temperature. |
|---|---|---|---|---|---|---|---|
| | 1. | 2. | 5. | 6. | 8. | 9. | |
| | °C. | °C. | °C. | °C. | °C. | °C. | °C. |
| Group I: | | | | | | | |
| Steer No. 2 | 33.7 | 33.5 | 33.2 | 33.4 | 34.0 | 34.0 | 33.6 |
| Steer No. 4 | 32.0 | 33.2 | 32.8 | 32.7 | 32.9 | 34.3 | 33.0 |
| Steer No. 5 | 34.2 | 34.1 | 33.9 | 33.5 | 33.0 | 33.5 | 33.7 |
| Group II:[2] | | | | | | | |
| Steer No. 3 | 32.2 | 31.6 | 32.1 | 31.8 | 32.3 | 33.6 | 32.3 |
| Steer No. 7 | 31.6 | 30.6 | 32.8 | 32.6 | 31.5 | 33.0 | 32.0 |
| Steer No. 10 | 33.3 | 32.2 | 33.6 | 31.5 | 32.7 | 32.6 | 32.6 |
| Steer No. 11 | 33.3 | 32.8 | 32.0 | 33.0 | 32.7 | 33.8 | 32.8 |
| Group III: | | | | | | | |
| Steer No. 6 | 32.9 | 32.5 | 33.1 | 32.8 | 32.7 | 33.8 | 32.9 |
| Steer No. 8 | 34.3 | 33.7 | 34.1 | 32.5 | 33.2 | 33.6 | 33.6 |
| Steer No. 9 | 32.2 | 32.0 | 33.4 | 32.7 | 32.0 | 33.1 | 32.6 |
| Steer No. 12 | 32.1 | 31.1 | 32.3 | 31.9 | 31.1 | 32.4 | 31.8 |
| Average | 32.9 | 32.5 | 33.0 | 32.6 | 32.6 | 33.4 | 32.8 |

[1] See Fig. 24, p. 182, for exact locations.

[2] Steer 1 was in the respiration chamber at the time these measurements were made.

for without such a record we can not adequately compare our results with the interesting data reported by Wood and Hill regarding the skin temperature and fattening capacity in oxen.[a] Their general conclusion is that the animals classed by them as "bad doers," that is, those that were not laying on flesh rapidly, had in every case a higher skin temperature than the average of the eight "good doers." Since on May 5 none of our animals were laying on flesh—indeed, all but the normals were losing flesh—direct comparison is hardly possible.

The deduction to be drawn from the data on our animals is that the 3 control steers showed in general a slightly higher average skin temperature than did the undernourished animals, with the single exception of steer 8, whose average skin temperature of 33.6° C. is about as high as the average temperature found with the 3 normal animals. However, this slightly higher skin temperature noted with the 3 control animals can hardly be taken as a sharply

[a] Wood and Hill, Journ. Agric. Sci., 1921, 6, p. 252.

established physiological fact, but is to be looked upon more as an indication of the probability of a slightly higher skin temperature with the better-fed or better-nourished animals. It is obvious that further investigation (it will be noted that this series of measurements was confined to one day only) will be necessary before any definite statement can be made regarding this point.

### The Pulse-rate of Steers.

Although our observations were not undertaken primarily with an object to contribute pulse-rate data to the study of the physiology of steers, in connection with our metabolism studies we deemed the measurement of the pulse-rate to be of importance. The pulse-rate or, more properly speaking, the heart-rate, is an index of the relative amount of circulatory activity, and as the blood carries oxygen to the tissues and brings back carbon dioxide to the lungs, the heart-rate may be taken as a crude, approximate index of relative metabolic intensity. It is thus a common observation that the pulse-rate increases with exercise and rapidly returns to the normal rate after exercise ceases. This is, of course, a well-known phenomenon with humans, and, indeed, with animals generally, and has been used as an index of fitness of the horse by Lützow.[a] Thus, with gross changes in metabolic activity there are gross changes in pulse-rate. When there are but minor changes in activity, however, the pulse-rate does not invariably change, for it must be remembered that the relationship between the heart-rate and metabolic activity is dependent upon the oxygen-carrying power of the blood and the volume output of the heart per beat, as well as the rate of heart-beat per minute and when the muscular activity is not excessive, such as the slight muscular activity involved in a change of body position, such activity is not necessarily always accompanied by a corresponding increase in pulse-rate. Indeed, according to the experience of the Nutrition Laboratory with men when walking, an experience first called to attention by Benedict and Murschhauser[b] and later confirmed with special evidence by Henry Monmouth Smith,[c] it was found that with ordinary walking on a level the muscular activity might be such that the total metabolism could increase twofold or even threefold, with not only no increase in the pulse-rate as compared with that measured while the subject was standing, prior to walking, but in many instances an actual decrease. Still, the pulse-rate is very extensively used as an index of metabolic activity. Fevers are almost invariably accompanied by an increase in pulse, and in making normal metabolism measurements with humans it is a standard routine to take the pulse-rate prior to the experiment, to insure that the subject is in a normal condition.

What is the situation with regard to the heart-rate of cattle and how is the heart-rate influenced by variations in the plane of nutrition? Reference to our technique for determining the heart-rate of our steers (see p. 74) will show that we recognized that certain factors influence the pulse-rate, such as activity, apprehension, eating, and, indeed, rumination. Every effort was made to avoid these extraneous influences when taking the pulse-rate. The factors of eating and rumination were particularly difficult to control (espe-

[a] Lützow, Deutsch. landw. Presse, 1909, 36, p. 245.
[b] Benedict and Murschhauser, Carnegie Inst. Wash. Pub. No. 231, 1915, p. 85.
[c] Smith, Carnegie Inst. Wash. Pub. No. 309, 1922, p. 166.

cially the latter) in those periods when full feed was given, but the majority of our measurements were taken under conditions that ruled out activity, apprehension, eating, or rumination. Pulse-rates were always taken with the animal in the standing position. It is perhaps to be regretted that we can not contribute positive evidence with regard to the difference in the pulse-rates of cattle while lying and standing, as this would give a clue to the probable difference in metabolism, a point that is by no means clearly established. At the moment of writing pulse-counts are being secured at Durham under exactly these conditions.

### DAILY PULSE-RECORDS AT DIFFERENT NUTRITIVE PLANES.

Ruling out the four factors just mentioned, it is obvious that our study of pulse-rate is especially well designed to note the influence, if any, of profound alterations in the nutritive plane upon the metabolic level. This study involves, therefore, measurements of the pulse-rates of the animals prior to any change in ration. While we had to content ourselves with but one day's observation of the standard metabolism in the case of the respiration experiments, we secured pulse data on steers 1 to 12 for 4 days prior to the first ration curtailment and, indeed, for nearly every day throughout the entire period of experimentation, even with steers 6 and 9 when on pasture. It is deemed unnecessary to print all these data, although we know of no investigation in which the pulse-rates of cattle have been as extensively studied as in this particular research. Because of lack of space, however, we are presenting in Table 48 only a few typical daily pulse-records of steers 1 to 12 at the different nutritive planes, giving, first, the data for December 18 to 27, inclusive, as this period includes 4 normal days and 5 days immediately following the drastic curtailment in ration, a curtailment amounting to one-half of the maintenance ration with Group II and one-third with Group III. We have likewise given the data secured during the last days of the period of submaintenance, namely, from April 28 to May 5, inclusive, as this period represents nearly the lowest metabolic level. Then, to note the influence of realimentation, and particularly the transition phase, we have given the data obtained from May 6 to 19, inclusive. Finally, as an index of the pulse-rates of these animals in the morning, when on full feed, we have included the period from August 19 to 25, inclusive. The footnotes to the table indicate those pulse-rates measured while the animal was ruminating and in a few instances while actually eating. Those cases where data are lacking are to be explained by the fact that no records could be secured, since the animals were inside the respiration chamber.

The pulse-records with steers 1 to 12 were taken about 10 a. m., after the steers had cleared up all their feed and about an hour before they were given water. It is important to note, therefore, that these records do not necessarily represent the *basal* pulse-rates of standing steers, since they were all taken after the animals had received feed or while feed was in the stomach. Since they were taken at essentially the same time, however, and since all of the animals, especially during the normal period, were living upon proportionately the same amount of hay, they are of great importance for comparative purposes. With this explanation we may pass immediately to a consideration of the influence of the curtailment of ration upon the pulse-rate,

TABLE 48.—*Daily pulse-rates*[1] *per minute at different nutritive planes, steers 1 to 12.*

| Character of ration and date (1918–19). | Group I. | | | Group II. | | | | | Group III. | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 2 | 4 | 5 | 1 | 3 | 7 | 10 | 11 | 6 | 8 | 9 | 12 |
| Maintenance: | | | | | | | | | | | | |
| Dec. 18 | 43 | 49 | 41 | 40 | 45 | 46 | 48 | 41 | 41 | 44 | 46 | 45 |
| Dec. 19 | 41 | 39 | 41 | 43 | 43 | 44 | 41 | 43 | 42 | 43 | 46 | 44 |
| Dec. 20 | 45 | 39 | 39 | 39 | 41 | 46 | 38 | 43 | 41 | 49 | 46 | 53 |
| Dec. 21 | 47 | 44 | 44 | 38 | 46 | 43 | 41 | 44 | 41 | 45 | 43 | 44 |
| First week submaintenance, Groups II and III; maintenance, Group I: | | | | | | | | | | | | |
| Dec. 23 | 50 | 48 | 45 | 37 | 34 | 39 | 38 | 41 | 39 | 41 | 50 | 42 |
| Dec. 24 | 50 | 48 | 42 | 28 | 40 | 32 | 34 | 40 | 43 | 44 | 47 | 44 |
| Dec. 25 | 54 | 50 | 42 | 28 | 34 | 35 | 37 | 38 | 44 | 38 | 41 | 38 |
| Dec. 26 | 52 | 48 | 40 | 26 | 35 | 34 | 38 | 40 | 40 | 36 | 38 | 40 |
| Dec. 27 | 46 | 48 | 40 | 28 | 31 | 34 | 32 | 38 | 40 | 36 | 38 | 40 |
| End of submaintenance, Groups II and III; maintenance, Group I: | | | | | | | | | | | | |
| Apr. 28 | 48 | 44 | 40 | 20 | 32 | 32 | 36 | 32 | 34 | 32 | 36 | 30 |
| Apr. 29 | 42 | 48 | 40 | 30 | 30 | 28 | .... | [2]44 | 32 | 40 | [2]40 | 28 |
| Apr. 30 | 36 | 40 | 40 | 24 | 32 | 28 | 40 | .... | 32 | 36 | 48 | 28 |
| May 1 | 48 | 40 | .... | 24 | 28 | 28 | 32 | 36 | 32 | [2]36 | 32 | 32 |
| May 2 | 48 | 48 | 48 | 24 | 32 | 28 | 32 | 32 | .... | 34 | 40 | 34 |
| May 3 | [2]52 | 48 | 44 | 24 | 32 | 28 | .... | 32 | 36 | 30 | .... | 28 |
| May 4 | 50 | 44 | [2]56 | 26 | 32 | [3]36 | 48 | 36 | 44 | 36 | [2]44 | .... |
| May 5 | 44 | 46 | 44 | .... | 28 | 28 | 34 | 36 | 36 | 36 | 36 | 32 |
| First week fattening on hay alone, Groups II and III; maintenance, Group I: | | | | | | | | | | | | |
| May 6 | 42 | 44 | 44 | .... | 32 | 36 | 40 | [2]42 | 40 | 40 | 34 | 32 |
| May 7 | 48 | [2]48 | .... | 28 | [2]40 | 36 | 34 | 36 | 36 | 40 | 44 | 36 |
| May 8 | [2]48 | .... | [2]46 | [2]40 | 40 | [2]44 | .... | 48 | 42 | [2]48 | 44 | 46 |
| May 9 | [2]52 | .... | 48 | [2]44 | [2]44 | 40 | 48 | 52 | [2]46 | 48 | 48 | [2]44 |
| May 10 | .... | 52 | [2]52 | 42 | [3]56 | 44 | [3]48 | [3]54 | [3]52 | [3]60 | [3]50 | [3]52 |
| May 11 | 44 | [2]56 | [2]52 | 32 | [3]48 | 36 | [3]48 | [2]52 | [2]52 | [3]48 | 46 | [2]48 |
| May 12 | 48 | [2]52 | 48 | 36 | [2]52 | 36 | 44 | 48 | [2]52 | .... | 48 | 36 |
| Fattening on hay and grain:[4] | | | | | | | | | | | | |
| May 13 | 48 | [3]64 | [3]60 | [3]48 | [3]60 | 56 | [2]56 | .... | [3]52 | [3]64 | [3]60 | [2]52 |
| May 14 | 48 | 56 | 56 | .... | 56 | 36 | [2]52 | 48 | 48 | 48 | [2]60 | .... |
| May 15 | [2]50 | [3]64 | .... | 36 | [2]60 | 48 | 44 | [2]48 | 56 | 52 | 60 | 48 |
| May 16 | [2]48 | [2]48 | [2]60 | [3]48 | 44 | [3]52 | .... | [2]44 | [2]44 | [2]52 | 60 | [3]56 |
| May 17 | 50 | 50 | [3]64 | [2]52 | [2]60 | 48 | [3]52 | [3]56 | [2]60 | [3]64 | 60 | [3]64 |
| May 18 | 56 | 64 | 64 | 60 | 60 | 48 | 48 | 60 | 60 | 64 | 68 | 64 |
| May 19 | 60 | 56 | [3]64 | [2]60 | [2]64 | [2]56 | 48 | 48 | 68 | [2]64 | 73 | 56 |
| Fattening on hay and grain:[4] | | | | | | | | | | | | |
| Aug. 19 | 64 | [3]88 | 68 | 62 | [3]80 | 72 | [2]85 | 76 | [2]60 | [2]88 | [2]62 | [2]80 |
| Aug. 20 | 60 | 88 | 74 | [2]64 | [3]84 | 72 | [3]68 | 80 | [2]68 | [2]84 | [2]64 | [2]84 |
| Aug. 21 | 60 | [3]88 | [2]76 | 56 | [2]80 | [2]74 | 72 | [3]84 | [2]56 | [2]88 | [2]60 | [2]88 |
| Aug. 22 | [2]58 | [2]88 | [2]72 | 76 | [2]80 | [2]80 | 76 | [2]84 | 50 | [2]86 | 56 | [2]84 |
| Aug. 23 | 58 | [3]88 | 68 | 60 | [2]72 | 76 | [2]84 | [2]82 | 56 | 86 | 58 | [2]85 |
| Aug. 24 | 52 | [2]84 | 72 | 78 | 78 | [2]78 | 78 | 72 | [2]56 | 80 | [2]56 | [2]80 |
| Aug. 25 | [2]46 | [3]88 | [2]72 | [2]58 | 76 | [2]68 | 64 | [2]70 | 60 | [2]72 | [2]74 | [2]76 |

[1] Pulse-rates were taken at 10 a. m., after the steers had cleared up all their feed and about an hour before they were given water.

[2] Steer ruminating while pulse-rate was being taken.

[3] Steer eating while pulse-rate was being taken.

[4] Steers 6 and 9 were on pasture from May 13 to Oct. 28, inclusive; steer 10 received a maintenance amount of hay alone, from May 6 to July 7, inclusive; steer 2 was on pasture from May 20 to Aug. 28, inclusive.

as exhibited by the values for December 23 to 27, inclusive, remembering that with Group II the ration was cut on December 22 to essentially one-half of their former ration, while with Group III it was cut to about two-thirds at the start, but that with Group I there was no feed restriction.

In Table 48 the first four records, i. e., for December 18 to 21, inclusive, represent what may be termed "normal" pulse-rates, as the curtailment in ration did not occur until December 22. The pulse-rates of steers 2, 4, and 5 show no essential change throughout the week following December 22, but with steer 1 there is a profound drop on December 24 of practically 10 beats. With steer 3 a decreased rate is evident on December 23, with a distinctly lower value at the end of this period, i. e., on December 27. With steer 6 there can be said to be practically no change for the 5 days following the curtailment of ration over the 4 days before. Steer 7 shows a decided drop, as does steer 8, but with this latter animal the decrease does not appear until December 25. Steer 9 shows a decrease, but this is not strikingly evident until December 25 and thereafter. Steer 10 shows a distinct drop, and steers 11 and 12 both a slight decrease. On the whole, therefore, the picture is clearly one of a noticeable drop in pulse-rate immediately following the curtailment of ration, most marked perhaps in the case of steer 1. It is, however, important at this point to note that steer 1 had a pulse-rate of 28 beats or below for 4 days, a value not recorded with any of the other animals. Indeed, the lowest value found with any other animal at this period is 31 beats with steer 3 on December 27.

About 4 months later, April 28 to May 5, at the end of the long submaintenance period, we find the pulse-rates for the control steers, Nos. 2, 4, and 5, are essentially like those at the beginning, the records being somewhat complicated, however, by rumination. But with all the animals on curtailed rations we find very great decreases over the original records during the maintenance period of December 18 to 21. The lowest level is noted with steer 1, which had given an indication of a low pulse-rate even during the first 5 days after ration curtailment. Steer 7 likewise shows a preponderance of results below 30, while steer 6, which showed hardly any effect during the first 5 days, now shows for the most part distinctly lower values.

Attention is here called to the several metabolism charts (see Figs. 25 to 27 and 30 to 38, pp. 235 to 287) which depict the general course of the pulse curves. As recorded on the charts, these curves are not, however, plotted directly from the data in Table 48, but represent weekly averages. They do not, therefore, show the almost immediate effect of the curtailment of ration noted on December 23 and are not particularly advantageous in showing the influence of realimentation on May 6. During the period from May 6 to 12 the animals in Groups II and III received essentially double the amount of hay given in the submaintenance period, while the animals in Group I continued to receive their maintenance amount of hay. The pulse-records are complicated here by the factors of eating and rumination, but the evidence would seem to indicate an increase in pulse-rate with all of the animals during this realimentation period with hay alone. In the next period, from May 13 to 19, when all the animals, including Group I, were receiving fattening rations of both hay and grain, the pulse-rates are in practically all cases perceptibly higher. Finally, the pulse-records for the period of heavy feeding from

TABLE 49.—*Daily pulse-rate[1] per minute, steers A and B.*

| Date. | Steer A. | Steer B. | Date. | Steer A. | Steer B. | Date. | Steer A. | Steer B. | Date. | Steer A. | Steer B. |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 1919. | | | 1920. | | | 1920. | | | 1920. | | |
| Dec. 28 | 56 | 54 | Feb. 15 | 36 | 32 | Apr. 4 | 34 | 34 | May 23 | 38 | 36 |
| 29 | 54 | 55 | 16 | 36 | 38 | 5 | 34 | 36 | 24 | 36 | 42 |
| 30 | 52 | 54 | 17 | 36 | 36 | 6 | ..... | 36 | 25 | 48 | 48 |
| 31 | 54 | 46 | 18 | 36 | 36 | 7 | 40 | 32 | 26 | 38 | 40 |
| 1920. | | | 19 | 34 | 36 | 8 | 36 | 36 | 27 | 38 | 42 |
| Jan. 1 | 54 | 54 | 20 | 34 | 32 | 9 | 34 | 36 | 28 | 48 | 42 |
| 2 | 56 | 52 | 21 | 37 | 34 | 10 | 32 | 36 | 29[5] | 40 | 36 |
| 3 | 50 | 48 | Av. | 36 | 35 | Av. | 35 | 35 | Av. | 41 | 41 |
| Av. | 54 | 52 | Feb. 22 | 34 | 36 | Apr. 11 | 34 | 34 | May 30[5] | 44 | 46 |
| Jan. 4 | 50 | 48 | 23 | 36 | 36 | 12 | 32 | 36 | 31 | 48 | 48 |
| 5 | 50 | 52 | 24 | 38 | 36 | 13 | 32 | 36 | June 1 | 50 | 50 |
| 6 | 50 | 52 | 25 | 36 | 36 | 14 | 36 | 36 | 2 | 50 | 52 |
| 7 | 45 | 48 | 26 | 37 | 36 | 15 | 36 | 36 | 3 | 51 | 48 |
| 8 | 40 | 44 | 27 | 38 | 38 | 16 | 37 | 36 | 4 | [3]52 | 50 |
| 9 | 56 | 52 | 28 | 32 | 32 | 17 | 33 | 32 | 5 | 46 | [3]52 |
| 10[2] | 52 | 50 | Av. | 36 | 36 | Av. | 34 | 35 | Av. | 48 | 49 |
| Av. | 49 | 49 | Feb. 29 | 36 | 38 | Apr. 18 | 32 | 30 | June 6 | 52 | 54 |
| Jan. 11[2] | 44 | 40 | Mar. 1 | 38 | 38 | 19 | 38 | 36 | 7 | 48 | 50 |
| 12 | 36 | 36 | 2 | [3]46 | 40 | 20 | 36 | 34 | 8 | 50 | 52 |
| 13 | 36 | 37 | 3 | 34 | 34 | 21 | 36 | 36 | 9 | 52 | [3]60 |
| 14 | 36 | 38 | 4 | 36 | 34 | 22 | 36 | 37 | 10 | [3]60 | 48 |
| 15 | 35 | 34 | 5 | [3]44 | 40 | 23 | 36 | 36 | 11 | 52 | [3]60 |
| 16 | 32 | 34 | 6 | ..... | ..... | 24 | 38 | 37 | 12 | 52 | 52 |
| 17 | 32 | 30 | Av. | 36 | 37 | Av. | 36 | 35 | Av. | 51 | 51 |
| Av. | 36 | 36 | Mar. 7 | 44 | 40 | Apr. 25 | 36 | 38 | Oct. 16 | 56 | 58 |
| Jan. 18 | 30 | 35 | 8 | 34 | 36 | 26 | 36 | 36 | 22[6] | 48 | 50 |
| 19 | ..... | ..... | 9 | 36 | 36 | 27 | 34 | 36 | 23 | 50 | 50 |
| 20 | 33 | 35 | 10 | 32 | 36 | 28 | [4]42 | 34 | 24 | 56 | 52 |
| 21 | 36 | 39 | 11 | 36 | 38 | 29 | 38 | 36 | 25 | 60 | 52 |
| 22 | 34 | 34 | 12 | 32 | 36 | 30 | 36 | 38 | 26 | 60 | 52 |
| 23 | 36 | 36 | 13 | 32 | 30 | May 1 | 36 | 35 | 27 | 60 | 52 |
| 24 | 36 | 32 | Av. | 35 | 36 | Av. | 36 | 36 | 28 | 60 | 54 |
| Av. | 34 | 35 | Mar. 14 | 36 | 34 | May 2 | 38 | 36 | 29 | 48 | 50 |
| Jan. 25 | 36 | 32 | 15 | 36 | 36 | 3 | 36 | 36 | Av.[7] | 55 | 52 |
| 26 | 36 | 32 | 16 | 32 | 36 | 4 | 36 | 33 | Oct. 30 | 56 | 56 |
| 27 | 36 | 30 | 17 | 32 | 36 | 5 | 38 | 36 | 31 | [3]66 | 56 |
| 28 | 36 | 30 | 18 | 32 | 34 | 6 | 34 | 36 | Nov. 1 | 60 | 50 |
| 29 | 36 | 36 | 19 | 30 | 34 | 7 | 36 | 48 | 2 | 64 | 60 |
| 30 | 36 | 36 | 20 | 40 | 40 | 8 | 36 | 38 | 3 | 64 | 60 |
| 31 | 36 | 34 | Av. | 34 | 36 | Av. | 36 | 38 | 4 | 65 | 64 |
| Av. | 36 | 33 | Mar. 21 | 44 | 36 | May 9 | [3]40 | 38 | 5 | 64 | 64 |
| Feb. 1 | 32 | 32 | 22 | 32 | 34 | 10 | 36 | 36 | Av. | 62 | 59 |
| 2 | 36 | 34 | 23 | 36 | 36 | 11 | 34 | 36 | Nov. 6 | 68 | 62 |
| 3 | 32 | 32 | 24 | 36 | 34 | 12 | 38 | 38 | 7 | 66 | 62 |
| 4 | 40 | 44 | 25 | 30 | 34 | 13 | 42 | [3]44 | 8 | 68 | 68 |
| 5 | 36 | 37 | 26 | 34 | 36 | 14 | 40 | [3]40 | 9 | 72 | 68 |
| 6 | 34 | 36 | 27 | 36 | 40 | 15 | 36 | 34 | 10 | 68 | [3]70 |
| 7 | 34 | 36 | Av. | 35 | 36 | Av. | 37 | 36 | 11 | [3]68 | [3]68 |
| Av. | 35 | 36 | Mar. 28 | 36 | 36 | May 16 | 38 | 36 | 12 | 44 | 48 |
| Feb. 8 | 36 | 38 | 29 | 36 | 36 | 17 | 36 | 44 | Av. | 64 | 62 |
| 9 | 36 | 32 | 30 | 36 | 36 | 18 | 40 | 32 | Nov. 13 | 60 | 60 |
| 10 | 34 | 32 | 31 | 44 | 40 | 19 | 40 | 36 | 14 | 62 | 64 |
| 11 | 36 | 37 | Apr. 1 | 36 | 34 | 20 | 38 | [3]44 | 15 | 68 | 68 |
| 12 | 36 | 36 | 2 | 32 | 33 | 21 | 36 | 42 | 16 | [3]72 | 68 |
| 13 | 36 | 38 | 3 | 36 | [3]40 | 22 | 36 | 36 | 17 | 70 | 72 |
| 14 | 36 | 32 | Av. | 37 | 36 | Av. | 38 | 38 | 18 | 72 | [3]76 |
| Av. | 36 | 35 | | | | | | | 19 | 72 | 76 |
| | | | | | | | | | Av. | 67 | 68 |

TABLE 49.—*Daily pulse-rate*[1] *per minute, steers A and B*—Continued.

| Date. | Steer A. | Steer B. | Date. | Steer A. | Steer B. | Date. | Steer A. | Steer B. | Date. | Steer A. | Steer B. |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 1920. | | | 1920. | | | 1920. | | | 1920. | | |
| Nov. 20 | 72 | 72 | Nov. 27 | 56 | 60 | Dec. 4 | 56 | 76 | Dec. 11 | 72 | 80 |
| 21 | 72 | 72 | 28 | 68 | 72 | 5 | 64 | 76 | 12 | 76 | 74 |
| 22 | 72 | 72 | 29 | 72 | [3]76 | 6 | 64 | [9]84 | 13 | 68 | 78 |
| 23 | 72 | 72 | 30 | 72 | 76 | 7 | 72 | 80 | 14 | 80 | 80 |
| 24 | 72 | 72 | Dec. 1 | 72 | 76 | 8 | 72 | [9]80 | 15 | 80 | 82 |
| 25 | 72 | 74 | 2 | 70 | 72 | 9 | 76 | [9]84 | 16 | [3]84 | 80 |
| 26 | 74 | 70 | 3 | 56 | 76 | 10 | 76 | [9]80 | 17 | 80 | [8]86 |
| Av. | 72 | 72 | Av. | 67 | 72 | Av. | 69 | 77 | Av. | 76 | 79 |

[1] Pulse-rates taken at 2 p. m. of the given date, at the end of the 24-hour period and just before the animal was weighed and given water.

[2] Both steers were fed 9,090 gm. hay per day on the average through Jan. 9–10; they were reduced to 4,545 gm. on Jan. 10–11.

[3] Ruminating; pulse-rate not included in average.

[4] Just after walking from respiration chamber; rise in pulse-rate probably due to exertion of walking; pulse-rate taken at $10^h15^m$ a. m. on this date; not included in average.

[5] On May 28–29 and for some time previous the steers had been getting 4,000 gm. hay per day on the average; on May 29–30 and to June 11–12 they received 9,090 gm. hay per day on the average.

[6] Between June 12 and Oct. 15 the steers were on pasture; fed on hay (amount not recorded) from Oct. 16 to Oct. 21, inclusive; on Oct. 22 they began to receive fattening rations of hay and grain.

[7] Not including Oct. 16.

[8] Steer had nail in foot; pulse-record not included in average.

[9] Steer caught horn in harness, which caused excitement; pulse-record not included in average.

August 19 to 25, although complicated again in many instances by rumination or eating, indicate a much higher level of heart-rate with practically all the animals, with the exception of steers 2, 6, and 9. These animals had been upon pasture for some time and their pulse-rates are essentially like those observed between May 13 and 19. The other animals receiving heavy grain rations for fattening purposes all show pronouncedly higher pulse-rates.

Although it was impracticable to give the individual pulse-rates for all four groups of the animals, so much of the detailed metabolism data are given for steers A and B that we have considered it desirable to present their pulse-records in detail. These daily records are accordingly given in Table 49, together with the weekly averages which have been used in plotting the pulse-rate curves of steers A and B in figures 41 and 42 (see pp. 297 and 298). Furthermore, while essentially the same phenomena are noted with regard to the pulse-rates of these two animals as were observed with steers 1 to 12, we have incorporated in the footnotes to the table data showing how the steers were fed for several days prior to and after the changes in ration, to facilitate the study of the influence of curtailment or augmentation of ration.

The initial normal values are followed by a pronounced fall on January 11, the first day after curtailment in feed. The heart-rate, however, never reaches the low level noted with one of the earlier animals, steer 1, but with both animals remains in the vicinity of 35 or 36 beats throughout practically the entire submaintenance period and with singular agreement, as is shown by the weekly averages. With the beginning of realimentation on May 29 there is an immediate increase in the heart-rate, shown definitely the first and especially the second and subsequent days, and the weekly average for the first week of realimentation is 7 to 8 beats higher than that for the week before. This increase continues regularly thereafter until the last week, from December 11 to 17, when the highest values of all were obtained.

Withholding feed had a very marked and immediate effect on the heart activity. This was counteracted somewhat during the first week of the submaintenance period by increased nervous irritability, which subsided after the first week or ten days when the animals gradually adapted themselves to the lowered standard of feeding. Withholding of the evening and morning meals preparatory to a respiration experiment was followed by a drop in pulse-rate, which again was followed by a proportionate increase when the steer was given his apportioned amount of feed. For example, the two steers *A* and B under normal feeding had practically the same pulse-rate, on the average varying between 49 and 54 beats per minute. Withholding feed entirely at the time of the evening meal on January 6 resulted in a lowered pulse-rate on January 7 with both animals, the drop amounting to 4 or 5 beats, followed by an additional drop of 4 or 5 beats on the next day, January 8, when the animals had been without feed for 48 hours. On the afternoon of January 8 they were fed the normal ration and on January 9 had a normal pulse-rate. At 2 p. m., January 10, the ration was cut from 9,090 to 4,545 grams of hay daily as a permanent ration, and by 2 p. m., January 12, the pulse-rate had dropped to 36 beats with both animals.

### RELATIONSHIP BETWEEN PULSE-RATE AND METABOLIC LEVEL.

While in general the relationship between pulse-rate and metabolic level is shown by the several curves presented in Figs. 25 to 27, 30 to 38, 41 and 42 (see pp. 235 to 298), a tabular presentation of the results is better for a direct comparison of the pulse-rates at the different nutritive planes. As will be seen

TABLE 50.—*Pulse-rate per minute at different nutritive planes, Group I.*

| Period. | Steer 2. | Steer 4. | Steer 5. | Notes. |
|---|---|---|---|---|
| Maintenance at start..... | 44 | 43 | 41 | Values are averages of the daily pulse-rates for Dec. 18 to 21. |
| Lowest level of maintenance. | 42 | 42 | 39 | Values represent average pulse-rates found at the lowest level of maintenance, i. e., with steer 2, Feb. 12 to 19; with steer 4, Feb. 17 to Mar. 12; with steer 5, Feb. 21 to 27. |
| Fattening..... | 72 | 84 | 75 | Values in the fattening period represent the maximum weekly average pulse-rates noted after May 6. |

later, steers 2, 4, and 5, although on supposedly maintenance rations, underwent a fairly considerable change in metabolic level, reaching an especially low point about the last 2 weeks in February. How was this metabolic level reflected in the pulse-rate? In Table 50 we have given the average pulse-rates, first, for the maintenance period at the start, i. e., for December 18 to 21, and second, for the lowest maintenance level of metabolism, which occurred at about the end of February. Finally, we have given the absolute maximum weekly averages noted during the fattening period. The initial maintenance values for the 3 steers in Group I are very close to 43 on the average. Singularly enough, at the very lowest maintenance level in the latter part of February, when the metabolism had very perceptibly fallen, the pulse-rates, although numerically one or two beats lower than during the initial mainte-

nance period, do not decrease at all in proportion to the profound drop in metabolism as measured. (See the discussion of gaseous metabolism, p. 245.) Finally, in the fattening period the pulse-rates are very much higher, in the case of steer 4 being exactly doubled.

It is more especially, however, with the animals which underwent ration curtailment that our interest lies, and accordingly in Table 51 we have recorded for Groups II, III, and IV the average pulse-rates at the initial maintenance level, at the lowest level of submaintenance metabolism, and finally, absolute maximum weekly average pulse-rates noted during the fattening period. While, as will be discussed in detail later (see p. 301), the metabolic level of steers 2, 4, and 5 had a distinct tendency toward the lower level noted with the animals on curtailed rations, without a corresponding decrease in the pulse-rate, we note in Table 51 that with all the animals in Group II there was

TABLE 51.—*Pulse-rate per minute at different nutritive planes, Groups II, III, and IV.*

| Group and steer No. | Maintenance. | Submaintenance (lowest level). | Fattening. | Notes. |
|---|---|---|---|---|
| Group II: | | | | The maintenance values are averages of the daily pulse-rates for Dec. 18 to 21 for Groups II and III, and Dec. 27 to Jan. 10 for Group IV. The submaintenance values represent average pulse-rates found at the lowest level of submaintenance, i. e., with steer 1, Feb. 12 to May 5; with steer 3, Feb. 6 to May 5; with steer 7, Mar. 11 to May 5; with steer 10, Feb. 13 to May 8; with steer 11, Feb. 8 to May 5; with all the steers in Group III, Feb. 8 to May 5; and with steers A and B, Jan. 10 to May 29. The values for the fattening period represent the maximum weekly average pulse-rates noted after May 6 with Groups II and III and after May 29 with Group IV. |
| Steer No. 1 | 40 | 25 | 66 | |
| Steer No. 3 | 44 | 30 | 80 | |
| Steer No. 7 | 45 | 31 | 82 | |
| Steer No. 10 | 42 | 35 | 79 | |
| Steer No. 11 | 43 | 33 | 76 | |
| Group III: | | | | |
| Steer No. 6 | 41 | 34 | 73 | |
| Steer No. 8 | 45 | 35 | 89 | |
| Steer No. 9 | 45 | 37 | 74 | |
| Steer No. 12 | 47 | 31 | 83 | |
| Group IV: | | | | |
| Steer A | 52 | 36 | 76 | |
| Steer B | 51 | 36 | 79 | |

a great fall in the pulse-rate during the submaintenance period. Thus, with steer 1 the pulse-rate fell from the maintenance level of 40 beats to 25 beats, the lowest value noted with any of our animals. Steer 10 showed the least drop in Group II, amounting to 7 beats. All the other animals in Group II showed pulse-rates lower by 10 or more beats per minute. During the fattening period with this group the pulse-rates were in every case increased two to nearly two and one-half times above the rates found at the lowest submaintenance level.

The peculiar action of the pulse-rate with steer 1 is worthy of special notice. His pulse-rate is the lowest of any of the steers in Group II on the maintenance level, is considerably lower than that of any of the steers in his group at the lowest level of submaintenance, and likewise is the lowest in the fattening period. In fact, the same holds true when he is compared with the steers in

Group III. While relatively the result of fattening in the case of steer 1 is to more than double the pulse-rate, as it does with all of the other animals in Group II, nevertheless it is a fact that his initial maintenance pulse-rate is increased only 26 beats or about one-half as a result of the fattening, while with most of the other animals the initial value is nearly doubled. Thus it would appear as if steer 1 reacted somewhat less to the fattening ration than did the other animals of Group II, and that we have here a very different individual, which might have been studied more in detail had the full significance of these pulse differences been realized at the time of observation.

With Group III the curtailment in ration was in two steps. The normal maintenance pulse-level is essentially that of the animals in Groups I and II, ranging between 41 and 47. In the submaintenance period from February 8 to May 5 this level has fallen with all the animals from 7 beats per minute with steer 6 to 16 beats per minute with steer 12, absolutely the lowest level of 31 beats being reached with this last animal. The low metabolism, therefore, is accompanied with all 4 of these animals by a very great lowering in heart-rate. On refeeding we note, as with Group II, that the submaintenance pulse-rate is doubled or more than doubled, being on the average about 80 beats per minute, while at the lowest level of submaintenance it is not far from 34 beats.

With steers A and B, Group IV, the situation is somewhat different, in that the maintenance pulse-rate from December 27 to January 10 was 52 and 51 beats, respectively, a level measurably higher than that noted with any of the other 12 steers. These 2 animals give an average of 52, while the 12 steers give an average of 43.[a] At the submaintenance level from January 10 to May 29, both animals reacted exactly alike on the average, the pulse-rate falling to 36 beats per minute, i. e., a level essentially that noted with Groups II and III in the lowest submaintenance period. In the fattening period the pulse-rate is more than doubled with both animals, being 76 with steer A and 79 with steer B, thus showing an intense reaction to the fattening rations. As a matter of fact, these high values of 76 and 79, as has already been pointed out, were obtained during the last week of the experiment, December 11 to 17.

From the course of the metabolism curves given for each of these 14 animals, (see Figs. 25 to 27, 30 to 38, 41 and 42, pp. 235 to 298) which show both the heat-production per square meter of body-surface and the pulse-rate per minute, it can be seen that the pulse-rate usually follows to a certain degree the metabolism. That is, when the pulse-rate is high the metabolism is quite inclined to be high; particularly is this true during the realimentation period. Likewise, exceedingly low pulse-rates and low metabolism values are found simultaneously. On practically every chart it will be noted that although the weekly average pulse-rates, as there plotted, have a tendency to decrease slowly as the undernutrition proceeds, the pulse-curves do not fall as precipitately as do those for the heat-production or for the body-weight. On the contrary, with refeeding the pulse-rate curve almost exactly parallels in most instances the curve for increasing body-weight and increasing heat-production. An explanation of this lack of harmony or parallelism of the curves at the begin-

[a] Colin (Traité de physiologie comparée des animaux, Paris, 1888, 2, p. 476) gives, as the average value of a large number of observations by veterinarians, a range of 45 to 50 beats per minute for the steer.

ning of the year as compared with the latter part of the year is not at present at hand. When we consider the metabolic levels in the gross periods of maintenance, submaintenance, and refeeding, the correlation between pulse-rate and metabolism is very striking, for we have already seen that on the maintenance level the pulse-rate is uniform for practically all animals, that during submaintenance, when the metabolism is very low by all methods of computation, the pulse-rate is at a very low level, and that during the period of refeeding, when the metabolism is very high, the pulse-rate is very high. In general, therefore, it can be stated that the pulse-rate and metabolism with steers are very closely in agreement, and arguing from the well-known relationship between the pulse-rate and metabolism of humans, particularly when the pulse-rates are measured upon the same person with different levels of metabolic activity, we can infer that with steers, when there is a change in pulse-rate with the same animal, there is a simultaneous change in metabolism which is roughly proportional to this change in the pulse-rate. This contention is of not insignificant value in supplementing some of the metabolism observations under special conditions, such as lying versus standing, and under conditions of temperature differences. The significance of this general observation is that a hint as to the metabolic activity of an animal, particularly of the same animal under different conditions, may be obtained by careful records of the pulse-rate. That the application of this general observation must not be carried to excess, however, is clear from the facts already established with men during horizontal walking. Every possible precaution should be taken to measure the pulse-rates under as nearly as possible ideal conditions, and in all metabolism measurements, particularly in measurements of the energy or gaseous metabolism, we believe the record of pulse-rate is an obligation upon experimenters that must not be disregarded.

### THE ABSOLUTE MINIMUM PULSE-RATE OF STEERS.

Practically all of our discussion thus far has been based upon weekly averages. But, as is shown in the description of the technique for recording the pulse-rate (see p. 74), each pulse-count is checked by 2 or 3 minutes' subsequent counting and hence may be considered to be a fairly well established figure. It is important, therefore, to note what were the actual minimum pulse-rates observed at any time throughout the experimental year with these animals. For this purpose we have examined very carefully all of our individual daily records and have given in Table 52 these minimum values with the dates when they were found, except when similar values were found on 3 or more days, in which case the dates are shown in the footnotes. As might be inferred from our earlier treatment of the pulse data, the lowest value of all was found with steer 1, which showed throughout the entire year a consistently low pulse-rate. His lowest value was 20 beats per minute, which is less than one-half of the average pulse-rate of animals measured under similar conditions and with maintenance rations. Nine of the 14 animals show pulse-rates of 28 or below. With both steers A and B the absolute minimum pulse-rate was 30 beats, which is a little higher than the minimum values found with any of the first year's groups of submaintenance animals.

We have inspected the figures very carefully to see if there is any possibility of correlating age with pulse-rate, but in vain. Likewise the matter of

temperature environment does not seem to be correlated with pulse-rate. It should be noted that steers A and B were studied during the second year, and while under identical conditions one with the other, they are not comparable to Groups I, II, and III, which were kept in another building and studied the year before. These first three groups were, however, all subjected to the same environment and studied at the same time, and hence are perfectly comparable. We regret extremely now that we did not secure pulse-counts of some of these steers while in the lying position. For example, the question arises as to whether the heart-rate of steer 1 while lying would have been less than 20 beats per minute. We have found very few records for warm-blooded animals of pulse-rates anywhere near as low as 20 beats per minute, and we feel that this value is quite comparable to the extraordinarily low value of 29 beats per minute observed in 6 different counts upon one of the men during the undernutrition investigation carried out at the International Y. M. C. A. College at Springfield, Massachusetts.[a]

TABLE 52.—*Absolute minimum pulse-rate per minute, Groups I, II, and III.*

| Group and steer No. | Date. | Minimum pulse-rate per minute. | Group and steer No. | Date. | Minimum pulse-rate per minute. |
|---|---|---|---|---|---|
| Group I: | | | Group III: | | |
| Steer No. 2 | Jan. 20 | 34 | Steer No. 6 | (1) | 28 |
| Steer No. 4 | Jan. 18 | 36 | Steer No. 8 | (2) | 28 |
| Steer No. 5 | Jan. 9 | 32 | Steer No. 9 | Feb. 21, 27 | 28 |
| Group II: | | | Steer No. 12 | Apr. 7 | 24 |
| Steer No. 1 | Apr. 28 | 20 | Group IV: | | |
| Steer No. 3 | Mar. 19 | 24 | Steer A | (3) | 30 |
| Steer No. 7 | Feb. 14 | 27 | Steer B | (4) | 30 |
| Steer No. 10 | Apr. 19 | 24 | | | |
| Steer No. 11 | Mar. 27 | 22 | | | |

[1] With steer 6 the minimum pulse-rate was found on 8 different days, i. e., Feb. 15, 16, 21, 23, and 28, Mar. 5 and 30, and Apr. 17.

[2] With steer 8 the minimum pulse-rate was found on 5 different days, i. e., Feb. 17, Mar. 1 and 3, Apr. 14 and 19.

[3] With steer A the minimum pulse-rate was found on 3 different days, i. e., Jan. 18, Mar. 19 and 25.

[4] With steer B the minimum pulse-rate was found on 5 different days, i. e., Jan. 17, 27, and 28, Mar. 13, and Apr. 18.

## GASEOUS METABOLISM AND ENERGY TRANSFORMATIONS.

### RESPIRATION EXPERIMENTS AS AN INDEX OF ENERGY REQUIREMENTS FOR MAINTENANCE.

The word "maintenance," which appears frequently in the discussions of animal and human nutrition, has several meanings. The definition of maintenance most applicable, in our judgment, to the conditions we are dealing with in this report, is that given by Professor H. P. Armsby, a definition so well phrased that we quote it in full.

"Feed is supplied to farm animals either that they may yield products useful to man as materials for human food and clothing or that they may serve him by the performance of mechanical work. But much as a factory must first be supplied with

[a] Benedict, Miles, Roth, and Smith, Carnegie Inst. Wash. Pub. No. 280, 1919, p. 387.

enough power to keep in motion the shafting, belting, and machinery in general before any product can be turned out, so the animal mechanism must be provided with sufficient feed to maintain the processes essential to life before any continued production is possible. The amount required for this purpose is called the maintenance ration of the particular animal. It is the quantity necessary simply to support the animal when doing no work and yielding no material product. A balance experiment with an animal receiving precisely a maintenance ration would reveal an exact equality between income and outgo of ash, nitrogen, carbon, hydrogen, and energy, showing that the body was neither gaining nor losing protein, fat, carbohydrates, nor mineral elements. From this point of view, maintenance might be characterized as a state of labile equilibrium between the anabolic and katabolic processes of metabolism."[a]

Our failure to secure nitrogen balance in steers A and B with the ration selected during period 1 has already been noted. By any process of computation, however, it is relatively simple to see that large losses of nitrogen *per se* have no particular relationship to changes in body-weight, that is, the loss of 1 kg. of flesh would correspond to a loss of but about 40 grams of nitrogen. The popular index of maintenance, certainly in ordinary gross feeding experiments, is the maintenance of body-weight. If the animal is kept at a uniform or reasonably uniform body-weight, he is stated to be on a "maintenance" ration. It is important to recognize that even if there are noticeable losses in weight, the animal might still be on maintenance, for losses in weight are by no means made up exclusively of organized body-tissue, and in the last analysis maintenance deals only with organized body-tissue. A loss of water with simultaneous balance of organized body-tissue is easily possible. The large mass of fill (with adult steers amounting to 60 kg.or more) is, strictly speaking, not a part of the animal organism as it has not as yet entered into the animal tissues, although it rests physically inside the alimentary tract. Any changes, therefore, in the composition or weight of fill are simply pooled in the daily changes in weight of the animal, and hence may lead to entirely erroneous conclusions.

By means of nitrogen-balance experiments, i. e., complete collection and analysis of excreta, and analysis of the feed ingested, one can determine whether there is a balance of protein or whether there is a gain or loss of protein. Since maintenance, in its more restricted and more sharply defined sense, relates to organized body-tissue, it is important to find, if possible, an index of changes in the organized body-tissue that will be as satisfactory in interpreting these changes as the nitrogen-balance is in determining the gain or loss of protein from the body. Clearly body-weight itself will not do. Even in periods as long as 2 weeks, as we have already observed, very great changes in body-weight are possible. If there is a persistent loss in body-weight over several weeks or months, one can reasonably infer that the ration is not sufficient for maintenance. An increase in weight over equally long periods suggests that the ration is in excess of maintenance and therefore productive.

Our specific interest in maintenance is, first and foremost, to be certain that the known factor in the balance, namely, food ingested, is equal to the body requirements. Food is required to sustain life and should be sufficient in amount and quality so that it will not be necessary to draw upon body

[a] Armsby, The nutrition of farm animals, New York, 1917, p. 267.

reserves for this purpose. Consequently it is extremely important, especially in critical physiological tests, to be able to tell whether a ration is a maintenance ration in the strictest sense. What is to be the criterion? While body-weight may serve the stockman's purpose admirably, it is obvious from what has already been stated that it fails as a true index of the gain or loss of organized body-tissue. In discussing extensively the general question as to whether the difference in live weight at the beginning and end of an experiment serves as a reliable index of the effect of the feed, Grouven, 60 years ago, gave one of the best criticisms showing the futility of using body-weight for this purpose, emphasizing as an important departure the substitution of respiration tests for body-weight records. He summarizes with the following explanation.

"Any opposition to such substitution is futile, since the indisputable fact remains that it would never become possible to explain the results of experimental feeding on the basis of scientific facts or to apply the results of experimental feeding successfully to general practice without a knowledge of the metabolic exchanges which take place in muscle tissue, fat, water, and mineral salts, a knowledge which can be obtained only by means of a respiration apparatus and metabolic balances."[a]

While the nitrogen-balance is a true index of the protein lost or gained, it is necessary to recognize that an index of the gain or loss of fat or carbohydrate from the body is equally important (quantitatively more so); and such an index, as Grouven points out, can be secured only with a respiration apparatus. The specific question then arises as to whether the carbon dioxide actually produced by an animal is greater or less than the carbon dioxide that theoretically could be produced from the digested feed. If it is greater, then there must be a loss of organic material; if it is less, there must be a storage of organic material. With the respiration apparatus only is it possible to strike a balance of the organic tissue other than protein and to determine definitely whether a given ration is or is not maintenance. Since most steers are fattened for market at an age when protein deposition has passed its maximum rate, a knowledge of the rate of fat deposition or, in other words, a knowledge of the carbon-balance is of the first importance.

Although Grouven's comment appeared in 1864, and bears just as pertinently upon the situation to-day as it did then, yet it is astonishing that so relatively few respiration chambers have been used for this purpose. When one considers the enormous sums spent by American and European governments in subsidizing agricultural research, the paucity of successful respiration apparatus for farm animals is almost alarming (two in America, one in Denmark, and two in Germany). It is of great interest, especially to Americans, that of these respiration apparatus, the one which has thus far yielded the most extensive and permanent results for the benefit of animal nutrition is the American apparatus at the Pennsylvania Institute of Animal Nutrition.

With the practical experience of the Nutrition Laboratory in referring to the nutritive state of humans for information regarding their general well-being and physiological fitness, it was no more than natural that any research in which this laboratory cooperated would need to have as a prerequisite some method for determining the gaseous metabolism of the animals studied, and for this purpose the apparatus at Durham was specifically designed. The

[a] Grouven, loc. cit., p. 574.

main object of the research at Durham was *not* to study pulse-rate, changes in body-weight, nitrogen-balances, and the amounts of drinking-water consumed and feces and urine excreted by these animals, important though these all are, but to study the energy requirements of animals at the different nutritive planes upon which we purposed placing them. At the very outset, therefore, it became important to find some suitable basis for the measurement of the energy metabolism of steers which would permit of intelligent and legitimate comparisons at the different nutritive levels.

PREREQUISITES FOR MEASURING THE "STANDARD METABOLISM" OF STEERS.

Although it is impossible here to go into an extensive discussion on the variations in nutritive plane as noted in man,[a] we may state that with humans the comparison of the metabolic levels is relatively simple. Long series of experiments have shown that certain conditions are recognized by physiologists as being suitable for comparative measurements on humans. These conditions are based upon the well-known fact that certain factors influence the metabolism noticeably. Thus, muscular activity during work may increase a man's metabolism 1,000 per cent, and consequently the metabolism should be measured during complete muscular repose, i. e., in the lying position. Secondly, the digestibility of food and the state of fill on a protein-rich diet may with man increase the metabolism over a short time by 40 per cent, and on an average diet may increase the metabolism over a considerable period of time by about 6 per cent. Consequently, basal metabolism measurements should be made after active digestion has ceased entirely, a condition which with mankind is attained about 12 hours after the last ingestion of food. An increase in body-temperature also affects the metabolism noticeably. Hence normal body-temperature is a prerequisite, and it is common, with humans at least, to insure that the temperature is not febrile. Furthermore, the psychic condition is not without influence, and every precaution is taken to minimize psychical disturbances with humans. This, however, presents a task which in many instances is not simple. In order to compare the metabolism of a normal adult man with that of an emaciated, undernourished child, one must be able to rule out all extraneous factors, and hence the above stipulations must obtain in all comparable experiments. Even then it has been found that the age element plays a very important rôle, and that one may not compare uncritically the metabolism of a child with that of an adult. Finally, the factor of sex must be taken into account, for women and girls have a measurably lower metabolism than men and boys of the same age and weight.

*Muscular activity and body position.*—From an examination of the prerequisites mentioned above, it is evident that it is absolutely impossible to control some of them in large ruminants. First and foremost comes the question of *muscular activity and body position.* While steers do lie down they are very prone, under experimental conditions, to stand. It is possible to make a steer stand the entire day by placing a chain under his neck between the stanchions so that he can not lie down. This is a common method. It is practically impossible to make a steer lie down for any great length of time, so that in

[a] For such discussion see Benedict, Miles, Roth, and Smith, Carnegie Inst. Wash. Pub. No. 280, 1919, pp. 192–204.

our experiments it became necessary to establish a new standard for our metabolism measurements and to give up one of the first prerequisites for *basal* metabolism, that is, complete muscular repose in the lying position. Even when standing, animals differ greatly in their activities, in spite of the narrow confines of a metabolism stall. One animal may stand very quietly while another may be quite restless, a restlessness that may vary from slight muscular movements only (as the weight is shifted) to somewhat excessive rubbing against the stanchion or the rather heavy lurchings of a steer irritated by the confinement of the respiration chamber. Between these great extremes naturally observations are of value only toward the lower border of activity. We attempted to use only animals that were quiet. We gave our steers special training to accustom them to the situation and did not accept the results of experiments when animals were unruly, as experiments under that condition have little, if any, value. The unreliability of ocular observation as to the degree of muscular repose led to the development of a graphic method for registering permanently the actual muscular state of these animals during experimental tests. This graphic method has been described in detail in the technical section of this report (see p. 54). Our experience has shown that this apparatus for recording the degree of activity can be adjusted so that it is supersensitive, and when so adjusted seemingly very great differences in activity, as recorded on this apparatus, may obtain without marked increment in the accompanying metabolism. On the other hand, when major activity is recorded, almost invariably we find it coincidental with increased metabolism and without the graphic demonstration of activity this increased metabolism would erroneously be ascribed to increased internal metabolic processes. Foregoing, therefore, periods of *complete muscular repose,* it became necessary for us to take as our first prerequisite periods when the animal was standing, with *minimum muscular activity,* as recorded on the kymograph drum. Exact quantitative measurement of the graphic tracings has proved impossible. The tracings are, however, of comparative value in interpreting metabolism data, particularly when high energy figures are present. Undoubtedly some other form[a] of apparatus less sensitive than that here employed would be more satisfactory for quantitative estimations of different degrees of activity.

*Digestibility of feed and state of fill.*—With ruminants, one of the most perplexing and difficult conditions is that produced by the ingestion of feed. While it is conventional with humans to consider that active digestion has ceased 12 hours after the last meal, such a consideration is far from the case with ruminants. The large mass of material in the fill furnishes a supply of feed which may be used for some time. Indeed, in his classic experiment on fasting steers, Grouven is convinced that the fill may furnish a not inconsiderable proportion of the daily needs for 3 or 4 days and that the true fasting metabolism of the steer is not actually reached until the fifth day. One of the most difficult problems, therefore, which we had to deal with in our tests was to determine at what stage in the digestive cycle we might logically consider a full-grown steer to be in a suitable condition for comparative experiments,

[a] Pott (Ohio Journ. Science, 1918, 18, p. 129) attached a pneumograph directly to the chest of the animal and was able from the kymograph tracings to detect many minor muscular movements.

knowing that 12 hours after the last feed is certainly not a sufficient length of time. As a rule, we made practically all of our tests 24 hours after the last ingestion of feed. It must be distinctly stated, however, that a steer in this condition is not comparable in any sense to a human in the post-absorptive state. Further discussion of the exact physiology of this stage of digestion will follow.

*Psychic and temperamental conditions.*—The placing of an animal, not accustomed to much handling and confinement, in almost utter darkness in a closed respiration chamber, and with other disturbing conditions imposed, such as a 24-hour fast, the humming of an electric fan and motor-driven blowers, and possibly the lowing of other animals in the barn, would seem at first sight to be capable of acting as psychic stimuli, even to the placid bovine, but as a matter of fact they soon get accustomed to such disturbances. Naturally, in working with 14 steers, temperamental differences were noted. Training was employed, in so far as possible, to overcome these differences, and in the interpretation of results all observations obviously affected by psychic disturbance of any kind, so far as we were able to measure it, were either rejected or included only with reserve and special comment. For the most part, however, this factor did not play any great rôle in our tests.

From the above considerations it is evident that our measurements of the metabolism of these animals were in no sense measurements of *basal* metabolism. What we sought was a *comparable condition for metabolism measurements*, a condition admittedly not basal, but, we trusted, sufficiently uniform to admit of its being used as a standard. Therefore, in speaking of our metabolism measurements, we will apply the term "standard metabolism," so long advocated by Krogh[a] as a substitute for "basal metabolism." In our particular case, however, we do not consider standard metabolism as in any sense comparable to or referable to basal metabolism, as this latter term is generally employed. Our prerequisites, therefore, for measuring the *standard metabolism* were that the animal should be studied 24 hours after the last feed, in the standing position, and in periods of least muscular activity. This last factor is by no means easy to express quantitatively, but our experimental conditions required that the activity indicated by the graphic record should at least not be pronounced. The records of activity were in many instances inconsistent with the actual metabolism measurements, and it frequently happened that where the metabolism measurement indicated a relatively low heat-output and the activity was seemingly of higher value, the experimental period was not rejected on the basis of the high activity recorded.

The post-absorptive condition is very difficult to realize with ruminants. The large amount of fill, the continuous fermentations that are going on, the prolonged, slow digestive activity continuing, as Grouven implies, for 3 or more days after feed is entirely withheld are factors which rule out the post-absorptive condition for ordinary work. Furthermore, most animals are at first uneasy and restless when feed is withheld, this uneasiness contributing to the disturbing factor of body activity. Accordingly, with the complete relinquishment of the idea of securing true basal measurements, our next step was to secure the best possible approximation of uniform, comparable,

[a] Krogh, The respiratory exchange of animals and man, London, 1916, p. 57.

or standard conditions. For this purpose, after obtaining reasonably standard conditions of muscular activity by insisting upon the standing position and using periods when muscular activity was noted to be at a minimum, we had left as our major difficulty the matter of digestive activity. It seemed at first that this problem could be in large part avoided. Drawing upon our experience with men, with whom the greatest rise in metabolism follows almost immediately on the ingestion of food, with a rather rapid return to basal after 6 or 7 hours, we felt that with our steers a fairly uniform digestive activity would obtain 24 hours after feed was given.

This is hardly the place to enter into a discussion of the true cause of the increase in metabolism coincidental with increased digestive activity, whether it is the work of handling the large bulk of food and fill in the intestines (the so-called "Verdauungsarbeit" of Zuntz), whether it is the specific dynamic action of foodstuffs as outlined by Rubner, or whether it is the stimulating action of acid bodies which are carried to the cells. Indeed, the true measure of the *increase* of metabolism due to feed ingestion with cattle is, in our judgment, far from being accurately determined and is the proper basis for an extended research. We have attempted to contribute toward this problem in a slight way with certain of our experiments, in which we have studied the metabolism after continued fasting. This is only a very small part of the problem, however. The most important part should follow, namely, a study of the metabolism after the ingestion of various amounts and qualities of feed. At the outset we must anticipate certain of our deductions and state that the results of our experiments do not seem to support the method of computing basal metabolism adopted by Professor Armsby and his associates, who, in studying two widely different amounts of the same feedstuff, noted the effect of the larger ration over the smaller, computed the effect per kilogram of the ration, and, computing therefrom the effect probably produced by the lower ration, deducted this from the metabolism as measured to find the basal metabolism. Our final prerequisite, therefore, for comparative measurements from the standpoint of digestion was that the animal should be studied 24 hours after the last ingestion of feed. This is seemingly justifiable, for our entire study was based upon a differential method, i. e., as to how the metabolism before curtailment in ration compared with the metabolism after curtailment in ration. The criticism, however, can immediately be raised that 24 hours after the ingestion of a large ration there may not be proportionately as low a carbon-dioxide production as 24 hours after the ingestion of a low ration. This possibility for error is freely granted, but it is necessary now for us first to examine carefully all the evidence available to support our use of the conditions outlined above as those for measuring our "standard metabolism."

### Carbon-dioxide Production as an Index of Total Metabolism.

From the description of the respiration chamber used in our research, it can be seen that as an index of total metabolism we relied solely upon the determination of the carbon dioxide given off by the animals. It is important, therefore, to consider to what extent this measurement may be used as an index of the true total energy transformations. In the metabolism of matter in the body oxygen is absorbed and carbon dioxide is produced. The

relationship between these two, the so-called "respiratory quotient," and more especially the amount of heat accompanying the development of each gram of carbon dioxide or the absorption of each gram of oxygen, is of utmost importance when the gaseous exchange alone is measured, and the heat must be computed therefrom. When carbohydrates are burned the respiratory quotient is 1.00, and when fats are burned it is practically 0.70. From the consideration of the heat of combustion of carbohydrates and fats it is easily computed that the heat per gram of carbon dioxide is very much greater when fats are burned than when carbohydrates are burned. If in the gaseous metabolism one refers the heat-production to the volume of oxygen consumed, it is seen that for every liter of oxygen entering into the oxidative processes there is produced essentially the same amount of heat, irrespective of whether fats or carbohydrates are burned.

This whole consideration is best illustrated by reference to Table 53, which gives the computed respiratory quotients for protein, fats, carbohydrates, and alcohol. Special attention is called to the respiratory quotient, and

TABLE 53.—*Respiratory quotients for protein, fats, carbohydrates, and alcohol.*

| Material. | Oxygen required to oxidize 1 gram. | | Produced in the oxidation of 1 gram. | | | Respiratory quotient. $\frac{CO_2 \text{ c.c.}}{O_2 \text{ c.c.}}$ | Heat. | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Weight. | Volume. | Carbon dioxide. | | Heat. | | Per gram oxygen. | Per liter oxygen. | Per gram carbon dioxide. | Per liter carbon dioxide. |
| | | | Weight. | Volume. | | | | | | |
| | *gm.* | *c.c.* | *gm.* | *c.c.* | *cal.* | | *cal.* | *cal.* | *cal.* | *cal.* |
| Starch..... | 1.185 | 829.3 | 1.629 | 829.3 | 4.20 | 1.000 | 3.54 | 5.06 | 2.58 | 5.06 |
| Cane sugar.... | 1.122 | 785.5 | 1.543 | 785.5 | 3.96 | 1.000 | 3.53 | 5.04 | 2.57 | 5.04 |
| Milk sugar[1].... | 1.066 | 746.2 | 1.466 | 746.2 | 3.74 | 1.000 | 3.51 | 5.01 | 2.55 | 5.01 |
| Animal fat..... | 2.876 | 2,013.2 | 2.811 | 1,431.1 | 9.50 | .711 | 3.30 | 4.72 | 3.38 | 6.64 |
| Human fat.... | 2.844 | 1,990.8 | 2.790 | 1,420.4 | 9.54 | .713 | 3.35 | 4.79 | 3.42 | 6.72 |
| Protein[2]..... | 1.367 | 956.9 | 1.520 | 773.8 | [3]4.40 | .809 | 3.22 | 4.60 | 2.89 | 5.69 |
| Alcohol..... | 2.085 | 1,459.5 | 1.911 | 972.9 | 7.08 | .667 | 3.40 | 4.85 | 3.70 | 7.28 |

[1] These values apply likewise to dextrose and levulose.

[2] While this computation is based upon meat protein, the values will be essentially the same for all proteins. These values represent quantities found when burning protein not in a calorimetric bomb, but in the animal body.

[3] The heat of combustion of protein averages 5.65 calories per gram; deducting the unoxidized material in the urine, the heat per gram would be 4.40 calories. For discussion of this point, see Atwater and Bryant, Storrs (Connecticut) Agr. Expt. Sta. Rept., 1899, p. 73. Since this value has to deal with protein actually burned, it is not to be confused with the value 4.1, commonly used to calculate the calories from ingested protein, of which a portion is assumed to be excreted undigested in the feces.

particularly to the heat per gram or per liter of oxygen and carbon dioxide, respectively. While the respiratory quotient may range from 0.667 with alcohol to 1.00 with starch and sugars, the heat per liter of oxygen ranges only from 4.60 calories with protein to 5.06 calories with starch, an extreme range of but about 10 per cent. If one takes into consideration the fact that the protein metabolism plays but a relatively small rôle in the entire human metabolism, and considers that the oxidation of fat results in the lowest heat-production per liter of oxygen, the range becomes only about 6 per cent. On the other hand, the range in the heat per liter of carbon dioxide is very great, for with alcohol there are 7.28 calories per liter of carbon dioxide and with milk sugar 5.01 calories; that is, the alcohol value is 45 per cent greater than that for milk sugar. Confining ourselves to the fats as one

extreme and milk sugar as the other, even on this basis the heat-production per liter of carbon dioxide resulting from the oxidation of fat is about 30 per cent greater than that from milk sugar.

It is thus apparent that the best index of the heat-production, when unknown amounts of mixed feed are being consumed, is undoubtedly the oxygen measurement. Indeed, at first sight it would seem quite hazardous to use the measurement of carbon dioxide for this index. Our justification for using carbon dioxide, considered solely from the standpoint of physiological chemistry, is, in the first place, that the ration of the ordinary domestic animal contains a large preponderance of carbohydrates with a relatively small amount of fat, except on special fattening rations, when such products as linseed and cottonseed meals are fed. Consequently, one would expect, *a priori*, to find the calorific value of carbon dioxide considerably nearer that for starches than that for fat. But by far the most important argument in favor of the use of the carbon-dioxide measurement alone is the actual experimental data on the relation between carbon-dioxide production and actually measured heat secured in the calorimeter of Professor Armsby, a detailed consideration of which will be given later.

To a certain extent the respiratory exchange of animals is of interest only in indicating the character of the material burned, as to whether it is predominantly fat or carbohydrate, and in furnishing a means for computing the energy metabolism. From the foregoing consideration of the respiratory quotients and the calorific values of carbon dioxide and oxygen, it is obvious that theoretically the oxygen consumption is a better index than the carbon-dioxide production, but that direct heat measurements have a still greater value. Unfortunately, heat measurements are extremely difficult to carry out. A calorimeter large enough for animals of this type is very complex. Indeed, the fact that even at this time there is but one successful instrument in the world is proof of this point. Professor Armsby succeeded in overcoming all technical difficulties and measured with utmost accuracy the direct heat-production of these large animals. No doubt the expense of this equipment and the large staff necessary for its operation precluded its general use. Another difficulty with direct calorimetry is the fact that with animals there are noticeable changes in body-temperature, and the amount of energy that may be thus temporarily stored in or lost from the body may represent a considerable proportion of the total. At present the methods of measuring these temperature differences are by no means so accurate as are the calorimetric appliances as a whole.

The oxygen measurement is by far the best index of heat-production. Indeed, with humans there is a very strong tendency at the present day to dispense entirely with direct calorimetric observations and to compute the heat-production from the exceedingly accurate oxygen measurements, because, irrespective of whether carbohydrate or fat is burned, the heat accompanying the absorption of 1 liter of oxygen in metabolic processes is essentially the same, the maximum difference being only about 6 per cent. Since it is very rare that in the post-absorptive condition the character of the material burned is exclusively carbohydrate on the one hand, or exclusively fat on the other hand, and since the combustion, in the human body at least, is usually made up of a mixture of carbohydrate and fat, with an average

respiratory quotient of 0.82, it can be seen that by the use of an average value for the heat per liter of oxygen (a value that is commonly taken, for clinical purposes at least, as 4.83), the possible error is reduced to a minimum. It is unfortunate, however, that with large ruminants the direct determination of oxygen is almost as difficult as the direct determination of heat. Thus far there are but two respiration chambers in which the direct measurement of oxygen has been successfully accomplished and the results published. Zuntz, with his marvellous technical and inventive genius, has devised a very elaborate respiration apparatus on the closed-circuit principle,[a] and he and his colleagues have reported 24-hour respiration experiments with a steer. Two 24-hour experiments were made in each of four feeding periods, and the oxygen measurements were made simultaneously with those of carbon dioxide, so that the respiratory quotient was thus determined in 8 experiments. Møllgaard and Andersen[b] have likewise determined the oxygen consumption directly in experiments with milch cows in their remarkably complete apparatus at Copenhagen.

Using the tracheal fistula, Zuntz and his associates have made many measurements of the respiratory quotients of large animals, as have likewise Møllgaard and Andersen, and Hagemann. An examination and comparison of the respiratory quotients, as determined by the tracheal fistula and the respiration chamber, is worthy of further consideration. Since the predominant nutrient in the ration of these large animals is carbohydrate, and as a whole we have to deal with a fat-poor ration, it is seen that, theoretically at least, most of the carbon dioxide would be derived from the combustion of carbohydrate with a respiratory quotient somewhat nearer 1.00 than that obtaining for fat, which is 0.70. This would be the case under practically all conditions, save where there is prolonged fasting. As yet, so far as we are aware, there are no published respiratory quotients for large animals when fasting. Grouven determined carbon dioxide only in his respiration chamber. Zuntz and his associates, Hagemann, and, indeed, Møllgaard and Andersen, were interested solely in the respiratory quotient under conditions of feeding. Armsby has for the greater part of his experimental work determined carbon dioxide alone of the gases, but has had the great advantage of being able to make direct heat measurements. Recently he informed us in a private communication that by applying the Jaquet principle to his apparatus, he succeeded in determining the oxygen consumption, but as yet no values for oxygen consumption have been published.

The fact that large amounts of carbon dioxide are produced by the processes of intestinal fermentation, unaccompanied by the absorption of oxygen, is a disturbing factor in interpreting the respiratory quotient measured on these large animals. Under these conditions there would be a pronounced tendency for the respiratory quotient to be abnormally high, and this must be taken into consideration in any interpretation of the quotients of animals with large ballast or fill. A striking illustration of this fact may probably be found in the comparison of the respiratory quotients obtained with the same animal when the measurements are made with a respiration chamber or by

[a] Von der Heide, Klein, and Zuntz, Landw. Jahrb., 1913, 44, p. 765.

[b] Møllgaard and Andersen, Kgl. Veterinaer-og Landbohøjskole Aarsskrift, Copenhagen, 1917, p. 195.

means of a tracheal fistula. Thus, Von der Heide, Klein, and Zuntz,[a] in discussing their eight 24-hour experiments, report that the respiratory quotients range from 1.029 to 1.147, all being above that for pure carbohydrate. In the same article,[b] in discussing the influence of rumination and of standing versus lying, they report a series of measurements made with the tracheal fistula by Klein on the same animal they had used in previous observations. These experiments were made during rumination in many instances, and in at least one case after very heavy feeding. In the first two experiments the respiratory quotient was 1.00, in the next one 0.97, and the 8 remaining quotients were all below 1.00, many of them below 0.87, the lowest being 0.766. When one compares these values, which will average well below 1.00, with the 8 quotients found in the 24-hour experiments by Zuntz and his associates, it can be seen that they are measurably lower. Since Klein's observations, however, were made during rumination and hence nearer the actual feeding-time, one would expect, *a priori*, that the quotients found by him would be higher than those found in the 24-hour experiments when the last 12 hours would be without feed, or at least feed would not be given continuously.

When a steer is studied inside a respiration chamber, there is contributed to the carbon dioxide therein a large amount of carbon dioxide produced by fermentation in the intestines. This increase in the carbon dioxide would automatically raise the respiratory quotient, since carbon dioxide from this source is produced without the accompanying absorption of oxygen. On the other hand, it is probably not correct to assume that all the carbon dioxide produced by fermentation in the intestines would pass out of the body through other channels than through the trachea. Undoubtedly a considerable quantity would enter into the gaseous exchange, as measured through a tracheal canula. In all probability, however, the striking difference in the respiratory quotients, as noted by the two methods, is to be explained in part by the intestinal fermentation.

Indeed, in their conclusions Von der Heide, Klein, and Zuntz lay great weight upon the disturbing factor of the carbon dioxide produced by fermentation, stating that the carbon dioxide resulting from fermentation in the intestinal tract amounts often to more than one-third of the total carbon dioxide excreted by the animal. They maintain that for this reason the carbon dioxide is an inaccurate measure of the true metabolism in ruminants, and that it therefore appears necessary to determine also the oxygen consumption of the animal.[c] In spite of the conclusion of Von der Heide, Klein, and Zuntz that it is necessary to determine the oxygen consumption, we nevertheless proceeded with the development of our apparatus for determining carbon dioxide alone, realizing that ultimately, perhaps, the determination of oxygen would be imperative.

For our specific purpose, therefore, it is important for us to abandon immediately all theoretical considerations as to the probability of a predominantly carbohydrate metabolism and the probability of the calorific value of carbon dioxide being nearer that for pure carbohydrate than that for pure fat, and pass immediately to a consideration of the facts demonstrated experi-

[a] Von der Heide, Klein, and Zuntz, Landw. Jahrb., 1913, 44, p. 804.
[b] *Ibid.*, p. 828.
[c] *Ibid.*, p. 831.

mentally by the remarkable series of researches carried out for a number of years by Professor Armsby. It was his data alone, uninfluenced by any theoretical considerations whatsoever, that gave us courage to proceed with the development, installation, and use of a respiration apparatus which would determine the carbon-dioxide production only of farm animals, from which measurement we believe the total energy transformations can be computed with a reasonable degree of accuracy.

### The Carbon Dioxide to Heat Ratio in Cattle.

Thanks to the extensive series of accurate experiments made by Professor Armsby and his associates, positive information is at hand with regard to the important ratio of the carbon dioxide excreted to the heat produced by cattle. A cursory examination of many of his extensive reports confirmed us in our belief that the ratio was sufficiently close to justify procedure along the lines of developing a respiration apparatus. Subsequently, Professor Armsby and his associates were good enough to make a more careful analysis of their data, and a report[a] has already appeared in which, based upon the measured heat-production and the carbon-dioxide elimination in 188 twenty-four-hour periods with cattle, they conclude that the heat per gram of carbon dioxide evolved is on the average $2.4947 \pm 0.0085$ calories, with a standard deviation of $0.1713 \pm 0.0060$ calorie. From a more careful analysis of all their data, in which the factor of the varying size of the animals was eliminated by computing all the results per kilogram of live weight, they propose three equations for computing the heat per gram of carbon dioxide. In these equations—

$x$ = air-dry weight of feed in grams per kilogram of live weight.
$y_1$ = calories of measured heat per kilogram live weight.
$y_2$ = grams of $CO_2$ per kilogram live weight.
$y_3 = \text{Heat}/CO_2 = y_1/y_2$.

(1) $y_1 = 0.869x + 14.176$.
(2) $y_2 = 0.455x + 4.365$.
(3) $y_3 = -0.0226x + 2.802$.

Special consideration is given by them to situations where minimum amounts of feed were consumed, but the important conclusion—in fact, the one upon which our whole venture was based—is the following:

"It would appear from the foregoing data that within the range of these experiments, i.e., with feed varying from 5 to 27 grams per kilogram live weight, equation (3) may be used for computing the $CO_2$ : heat ratio of cattle when their live weight and the amount of feed consumed are known, and that by the use of this ratio the heat-production may be computed from the observed $CO_2$ production with a good degree of accuracy, at least for animals on dry feed and not performing work."[b]

While practically all of the work from which these deductions were made was with steers during periods of approximately maintenance feeding, it was obviously a matter of considerable conjecture as to whether these deductions would apply under conditions as unusual as those obtaining in our experi-

[a] Armsby, Fries, and Braman, Proc. Nat. Acad. Sci., 1920, 6, pp. 263 et seq.
[b] *Ibid.*, p. 265.

ments, where the amount of feed was only one-half or less than one-half of the amount required for maintenance. Since the major part of our research was to be based essentially upon the differential method, that is, the difference between the metabolism when on maintenance feed and when on the low feed-level, and we were not primarily interested, for the time being at least, in absolute values, we were not deterred from continuing our research by the fact that at the time no undernourished or fasting animals had been studied by Professor Armsby. Fortunately, after our work was nearly completed, Dr. Armsby kindly furnished us (in a private communication) data regarding two fasting cows, and, furthermore, gave us his personal advice with regard to the best probable factors for the calorific value of carbon dioxide to be used in our experiments at the different nutritive planes. We feel, therefore, unusually well buttressed in our general thesis that the measurement of carbon dioxide alone is of great scientific value, although recognizing that the direct measurement of oxygen consumption, and more particularly direct heat-measurements, are of far greater scientific importance. But in lieu of the extraordinarily complicated plant required for direct heat-measurements and the apparatus and unusual technical skill required for the oxygen measurements, we feel that an apparatus determining carbon dioxide only has a distinct place in the very wide and, in large part, uncharted field of metabolism measurements on domestic animals.

### SELECTION OF THE CARBON DIOXIDE TO HEAT RATIOS USED IN OUR RESEARCH.

In the selection of carbon dioxide to heat ratios we have accepted those submitted in a private communication by Professor Armsby, ratios which he obtained in 1920–21 on 2 cows during the first 12 hours following 24 hours of fasting. The cattle entered the respiration calorimeter and the experiment began 24 hours after the last feed was given, the experimental periods being each 12 hours long. Consequently, the first 12-hour period inside the respiration calorimeter corresponds very closely to the period during which most of our experiments were made. During the first 12 hours after 24 hours of fasting, preceded by an approximately maintenance ration, these 2 cows showed heat ratios of 3.103 and 3.077, respectively, and in our computations we have accordingly used the round figure of 3.1 calories per gram of carbon dioxide. Since during the first few weeks our animals were on a supposedly maintenance ration, this factor of 3.1 calories is the best that seemingly could be used. With the curtailment in ration the question arises as to whether another factor should be used, and for this purpose we have reference to further unpublished data of Professor Armsby, who found that with his cows during the second 24 hours of fasting the factor was 3.146 calories and 3.254 calories, respectively, or an average of 3.2 calories. The approach to the fasting condition, therefore, is evidently rather rapid, for on reference to Table 53 (p. 201), it can be seen that if pure animal-fat combustion was taking place, the ratio would be 3.38. On curtailed rations our animals undoubtedly burned more body-fat than did Professor Armsby's cows during the first 24 hours of fasting, and possibly during the second 24 hours. It seems probable, however, that the value of 3.1 calories would obtain with our animals not only during the period of so-called "maintenance," but likewise during the

period of submaintenance, and we have also applied it to the short period of 1 or 2 weeks following submaintenance, when the steers were fed back on hay alone.

During the realimentation period excessive amounts of feed were given and consequently the ratio would fall. Had our measurements been made during the actual process of digestion, we would probably find figures as low as the average found by Professor Armsby of 2.37, obtained in experiments when the animal was fed regularly inside the chamber. This heat-ratio of 2.37 closely approximates that for pure carbohydrate, which is 2.55. Indeed, it is somewhat lower, thus suggesting the strong probability of a respiratory quotient higher than 1.00, i. e., formation of fat from carbohydrate, and consequently the liberation of carbon dioxide unaccompanied by oxygen consumption in the simple process of conversion of carbohydrate to fat.[a] Our experiments were rarely made during the actual process of digestion. In other words, the regular routine of beginning the experiment only 24 hours after the last feed makes it probable that a ratio not far from 3.1 is correct. On the other hand, that there should not be some influence of an excessively rich fattening ration upon this ratio even after 24 hours of fasting seems highly improbable, and we have therefore used 2.9 for the calorific value of a gram of carbon dioxide in all of our realimentation periods with both hay and grain. It is necessary to bear in mind, however, that these measurements were always made during a period beginning 24 hours after the last feed.

## Experiments upon the Factors Affecting Standard Metabolism.

Although it has been necessary with ruminants to modify the strict specifications commonly used in basal metabolism measurements on men and, indeed, lower animals, so that the term "standard metabolism" has been substituted for the term "basal metabolism," it is important, nevertheless, to recognize that all of the factors influencing the measurement of basal metabolism likewise obtain in measurements of the *standard* metabolism. Of these several factors that of muscular activity is the most prominent. The digestion of feed is another factor, and since the specifications for measuring standard metabolism do not preclude any influence of the digestion of feed (indeed, probably such influence is present to some extent), it is necessary in the elaboration and specific differentiations of our standard conditions to study the effect of the ingestion of feed.

### EFFECT OF MUSCULAR ACTIVITY.

Taking into consideration the first of these factors, namely, muscular activity, we have already emphasized the importance of securing minimum activity or the greatest degree of repose and have explained the use of the graphic method for recording the activity of these animals and the interpretation of the kymograph records. It will be of positive value in interpreting our other data to have some conception as to what is the maximum influence upon the standard metabolism of muscular activity of the kind that can be engaged in by a steer while inside a metabolism stall or a respiration chamber. In certain of our first experiments, when the animals were unaccustomed to the apparatus and were much irritated by the confinement, we had opportunity

[a] Fermentation processes with liberation of carbon dioxide would likewise produce this effect.

to make several observations upon the carbon-dioxide production during periods of great activity and during periods of comparative repose, both conditions being noted within a very short time, on a few occasions on the same day. We therefore have a method of estimating the possible effect of maximum stall activity. In Table 54 we have listed those instances which show an increase in the standard metabolism of over 25 per cent due to great muscular activity. Here it can be seen that the carbon-dioxide production per half hour may be increased 29 to 55 per cent as a result of excessive activity. In analyzing the character of the activity it can only be stated that there was

TABLE 54.—*Maximum increase in carbon-dioxide production caused by great activity.*
[Maximum and minimum periods on the same day.]

| Steer No. | Date. | Carbon-dioxide production per half hour. | | | Notes. |
|---|---|---|---|---|---|
| | | Maximum.[1] | Minimum.[2] | Increase, maximum over minimum. | |
| | | *gm.* | *gm.* | *p. ct.* | [1]Accompanied by great activity; not used in the final tabulation of results. |
| 1 | Jan. 30 | [3]78.8 | 60.5 | 30 | |
| 2 | Dec. 4 | 109.5 | 70.6 | 55 | |
| 2 | Jan. 8 | 113.3 | 86.3 | 31 | [2]Accompanied by minimum or moderate activity. |
| 3 | Jan. 10 | 96.8 | 74.9 | 29 | |
| 7 | Jan. 11 | 92.5 | 60.1 | 54 | |
| 10 | Dec. 5 | 125.4 | 91.3 | 37 | |
| 11 | Dec. 5 | 90.3 | 67.3 | 34 | [3]Steer kicked hard twice while this measurement was being taken. |
| B | Jan. 19 | 61.9 | 42.4 | 46 | |
| B | Mar. 30 | 75.3 | 57.1 | 32 | |

not infrequently considerable lowing. As the animals were confined with the plank stanchions indicated in Fig. 7, they could do themselves no injury, although they would exert themselves to the limit of their ability. Obviously under such conditions the energy spent could not be interpreted in terms of measured mechanical work done, yet to a certain extent the activities of the animal while in the stall may be compared directly to those of a crying, restless infant, lying in a crib, whose metabolism has been measured under this condition. The crying of an infant may increase the metabolism not only 29 or 55 per cent but, as one individual instance has shown, 211 per cent.[a] In this latter case probably not a small part of the increase in metabolism may have been due to the work of crying, for unquestionably the muscular efforts of severe crying must be very great. A side-light upon this point is thrown by the experiments made with a group of young women in a large respiration chamber of the Nutrition Laboratory,[b] not unlike that here described, where the metabolism was measured first while the young women were sitting quietly reading and again while sitting and reading aloud, and finally when sitting and singing. The increments in metabolism due to the difference in activity between sitting quietly reading and sitting and reading aloud were astonish-

[a] Benedict and Talbot, Carnegie Inst. Wash. Pub. No. 233, 1915, p. 111.
[b] Benedict and Johnson, Proc. Am. Philos. Soc., 1919, 58, p. 89.

ingly small, amounting to but 3 per cent on the average. When the same group of young women sang, the increment in metabolism was 22 per cent.

Other instances of activity with our steers show increments in metabolism considerably less than the increments of 29 to 55 per cent noted in Table 54, and as an approximate figure, based on all the measurements in our entire series, it may be stated that the stall activity of our steers could raise the standard metabolism 15 per cent on the average, with a maximum of 55 per cent. After the first week our steers were, as a rule, very much quieter, and our data show that after this period the activities never increased the standard metabolism above 25 per cent. Indeed, the difference between the maximum and minimum carbon-dioxide production in any given experiment did not usually exceed 15 per cent, and consequently the difference between the metabolism with ideal standard conditions and that with considerable activity would be usually not far from 15 per cent. It is important to bear this figure in mind in the subsequent analysis of our results.

### EFFECT OF PROLONGED FASTING AND OF INGESTION OF FEED.

Recognizing the difficulty of securing the post-absorptive condition in ruminants, we decided on the arbitrary specification of "24 hours after the last feeding." It is important in this connection to note the influence of prolonged withdrawal of feed, and certain of our experiments were made for the special purpose of throwing light upon this point. Admittedly they are very perplexing. Frequently they bring in the element of difference in temperature environment, and more frequently the element of restlessness and unequal muscular activities. We can by no means, therefore, state that these few preliminary experiments permit drawing mathematically exact conclusions with regard to this point. We believe, however, that our figures are worthy of presentation and do throw a certain amount of light upon the question. During the first year's work certain experiments were specifically made with 8 of the steers to study the influence of prolonged withdrawal of feed. The results are incorporated in Table 55,. which gives the interval between the ingestion of feed and the beginning of the experimental period, the average temperature of the chamber, and the average carbon-dioxide production per half hour and per 500 kg. of body-weight per half hour.

With steer 1 two such measurements were made, one on May 5 and 6 at the end of the period of low ration and the other on October 29 and 30, when he had gained in weight about 250 kg. Unfortunately the two experimental series are not comparable, for there is a very great difference in the muscular activity.[a] There is a distinct tendency, however, for the carbon-dioxide production per half hour and per 500 kg. of body-weight per half hour to become smaller as the fast progresses, both during the experiment in May and that in October. Steer 3 shows little, if any, change in the carbon-dioxide production, owing to irregular values at the thirty-third hour due to activity. Steer 7 similarly shows irregular values for the first three periods, but a distinctly low value at the fifty-second hour. Steer 10 shows a fall, steer 11 a pronounced drop from the twenty-eighth to the fifty-third hour, and steer 6 a similar pronounced drop. Steer 9 was brought in from pasture prior to the

[a] In this and subsequent tables the degree of activity is recorded as follows: I, quiet; II, moderately active; III, very active.

experiment. Here again a very noticeable decrease in the carbon-dioxide production per 500 kg. per half hour is noted between the twenty-seventh and the fifty-first hour. Steer 4 in May shows a slight decrease, and in July a much more pronounced decrease. In general, then, with but few exceptions

TABLE 55.—*Carbon-dioxide production 26 to 53 hours after feed, Groups I, II, and III.*

| Date (1919). | Group, steer No., and time of experiment. | Interval between feed and beginning of period. | Average temperature of chamber. | Body-weight. | Average carbon-dioxide production per half hour. | | Activity.[1] |
|---|---|---|---|---|---|---|---|
| | | | | | Total. | Per 500 kg. | |
| | Group I, Steer 4. | *hrs.* | *°C.* | *kg.* | *gm.* | *gm.* | |
| May 8 | 10h27m a. m. to 11h57m a. m. | 28 | 18.3 | 490 | 61.7 | 62.9 | I, II, II |
| | 3 08 p. m. to 4 38 p. m. | 33 | 21.7 | ..... | 60.1 | 61.3 | I, II, II |
| | 9 29 p. m. to 10 59 p. m. | 39 | 20.8 | ..... | 55.4 | 56.6 | I, II, III |
| May 9 | 10 32 a. m. to 12 02 p. m. | 52 | 18.6 | 471 | 53.0 | 56.3 | I, I, I |
| July 1 | 9 03 a. m. to 10 33 a. m. | 27 | 24.4 | 551 | 104.3 | 94.6 | III, III, III |
| | 2 39 p. m. to 4 09 p. m. | 32 | 30.6 | ..... | 91.3 | 82.8 | II, III, III |
| | 7 42 p. m. to 9 12 p. m. | 37 | 28.6 | ..... | 84.8 | 77.0 | III, III, III |
| July 2 | 9 00 a. m. to 10 30 a. m. | 50 | 23.2 | 532 | 77.6 | 72.9 | II, III, III |
| | Group II, Steer 1. | | | | | | |
| May 5 | 11h04m a. m. to 12h04m p. m. | 29 | 18.3 | 454 | 44.8 | 49.4 | I, I |
| May 6 | 8 52 a. m. to 10 23 a. m. | 50 | 16.7 | 441 | 41.1 | 46.6 | I, I, I |
| Oct. 29 | 8 33 a. m. to 10 03 a. m. | 26 | 17.8 | 691 | 93.6 | 67.7 | II, III, III |
| | 1 24 p. m. to 2 54 p. m. | 31 | 18.7 | ..... | 89.4 | 64.7 | II, II, III |
| | 7 50 p. m. to 9 20 p. m.[2] | 37 | 17.6 | ..... | 86.9 | 62.9 | II, II, II |
| Oct. 30 | 10 58 a. m. to 12 28 p. m. | 52 | 20.5 | 682 | 81.2 | 59.5 | I, II, II |
| | Group II, Steer 3. | | | | | | |
| Oct. 29 | 10h17m a. m. to 11h47m a. m. | 28 | 17.9 | 615 | 77.9 | 63.3 | II, III, III |
| | 3 05 p. m. to 4 35 p. m. | 33 | 20.0 | ..... | 95.4 | 77.5 | II, III, III |
| | 9 41 p. m. to 11 10 p. m. | 39 | 18.5 | ..... | 81.9 | 66.5 | II, II, II |
| Oct. 30 | 9 16 a. m. to 10 46 a. m.[3] | 51 | 17.6 | 583 | 81.0 | 69.5 | II, II, II |
| | Group II, Steer 7. | | | | | | |
| Oct. 27 | 11h02m a. m. to 12h32m p. m. | 29 | 20.8 | 592 | 91.9 | 77.7 | II, III, III |
| | 3 26 p. m. to 4 56 p. m. | 33 | 21.9 | ..... | 99.8 | 84.3 | II, III, III |
| | 10 00 p. m. to 11 30 p. m. | 40 | 20.0 | ..... | 86.0 | 72.6 | II, III, III |
| Oct. 28 | 10 40 a. m. to 12 10 p. m. | 52 | 19.1 | 551 | 65.2 | 59.2 | I, II, II |
| | Group II, Steer 10. | | | | | | |
| May 8 | 8h30m a. m. to 10h00m a. m. | 26 | 18.0 | 454 | 48.9 | 53.9 | I, I, I |
| | 1 19 p. m. to 2 49 p. m. | 31 | 18.5 | ..... | 49.0 | 53.9 | I, I, I |
| | 7 40 p. m. to 9 10 p. m. | 37 | 19.6 | ..... | 43.4 | 47.8 | I, I, II |
| May 9 | 8 46 a. m. to 10 16 a. m. | 50 | 18.6 | 443 | 43.0 | 48.6 | I, I, I |
| | Group II, Steer 11. | | | | | | |
| July 14 | 10h43m a. m. to 12h13m p. m. | 28 | 26.4 | 503 | 85.6 | 85.1 | I, II, II |
| | 3 35 p. m. to 5 05 p. m. | 33 | 29.9 | ..... | 76.1 | 75.7 | I, II, II |
| | 10 57 p. m. to 11 57 p. m. | 41 | 27.0 | ..... | 73.8 | 73.3 | II, II |
| July 15 | 11 10 a. m. to 12 40 p. m. | 53 | 26.9 | 469 | 58.7 | 62.6 | II, II, II |
| | Group III, Steer 6. | | | | | | |
| Oct. 27 | 9h19m a. m. to 10h49m a. m. | 27 | 18.7 | 471 | 70.7 | 75.0 | II, II, II |
| | 1 46 p. m. to 3 16 p. m. | 31 | 20.8 | ..... | 59.0 | 62.6 | II, II, II |
| | 8 14 p. m. to 9 44 p. m. | 38 | 19.1 | ..... | 61.5 | 65.3 | II, II, II |
| Oct. 28 | 8 51 a. m. to 10 21 a. m. | 51 | 18.5 | 460 | 45.2 | 49.1 | I, I, II |
| | Group III, Steer 9. | | | | | | |
| July 14 | 8h56m a. m. to 10h26m a. m. | 27 | 23.0 | 551 | 92.2 | 83.6 | II, II, II |
| | 1 53 p. m. to 3 23 p. m. | 32 | 28.0 | ..... | 90.4 | 82.1 | I, II, II |
| | 7 28 p. m. to 8 58 p. m. | 37 | 29.5 | ..... | 69.8 | 63.4 | I, II, II |
| | 9 15 p. m. to 10 45 p. m. | 39 | 26.1 | ..... | 76.0 | 69.0 | II, II, II |
| July 15 | 9 23 a. m. to 10 53 a. m. | 51 | 24.0 | 531 | 64.0 | 60.2 | I, I, II |

[1] I, very quiet; II, moderately active; III, very active.
[2] Steer kicked and split door of chamber during this period.
[3] Steer had been in respiration chamber all night.

the picture is that of a measurable decrease in the carbon-dioxide production with continued fasting beyond 24 hours after the last ingestion of feed.

In the most careful interpretation of the figures in Table 55 one should take into account the differences in muscular activity, which are by no means

inconsiderable. Likewise, one should recognize that there is sufficient evidence in the table to show that this decrease in metabolism, when feed is withheld for more than 24 hours, is dependent in large part upon the character and amount of the ration constituting the feed-level at the time the experiment is made. Thus, it can be seen that with practically all the animals when the observations were made in May 1919, i. e., during the period of low ration, the decrease in metabolism with fasting prolonged beyond 24 hours was relatively much less than when the tests were made later in the year during the period of full feed. Since by far the larger percentage of our tests were made with special reference to the influence of restriction of ration, i. e., under feed conditions similar to those obtaining in the May, 1919, experiments cited in Table 55, it can be seen that during the period of submaintenance feeding in all probability we had to deal with a relatively slight sliding scale of metabolism 24 hours after the ingestion of feed. Furthermore, if we had waited 48 hours we would probably have found a somewhat lower metabolism,

TABLE 56.—*Effect of ingestion of feed on the carbon-dioxide production.*

| Steer No. | Date. | Time of experiment. | Interval between feed and beginning of period. | Body-weight. | Average carbon-dioxide production per 500 kg. per half hour. | Activity. |
|---|---|---|---|---|---|---|
| | 1919. | | | *kg.* | *gm.* | |
| 3 | Feb. 6 | $8^h30^m$ a. m. to $10^h15^m$ a. m. | 26 hrs. | 430 | 55.5 | I, I, I, I |
| | | 10 45 a. m. to 12 11 p. m. | 11 mins.[1] | ..... | 59.9 | I, I, I |
| 6 | Feb. 5 | 8 16 a. m. to 10 46 a. m. | 26 hrs. | 390 | 63.6 | I, I, I, II, I |
| | | 11 29 a. m. to 2 00 p. m. | 14 mins.[2] | ..... | 62.9 | I, II, III, III, III |
| 8 | July 16 | 9 13 a. m. to 10 13 a. m. | 2 hrs.[3] | 474 | [4]163.3 | III, III |

[1] Steer ate 1.13 kg. hay between $10^h15^m$ and $10^h34^m$ a. m.
[2] Steer ate 1.13 kg. hay between $10^h46^m$ and $11^h15^m$ a. m.
[3] Steer ate 3.17 kg. hay and 5 kg. grain between $6^h30^m$ and 7 a. m. on July 16, and drank water *ad libitum*.
[4] On June 21, 24 hours after feed, steer 8 showed an average carbon-dioxide production per 500 kg. per half hour of 102.9 gm.; on June 27 of 112.6 gm.; on July 9, 99.7 gm. On July 16 no measurements were made 24 hours after feed.

but in all probability, when compared with the metabolism of the animal at the height of digestion, a drop nowhere near so low proportionately as that noted during the first 24 hours.

These figures do not give any information, however, as to how rapid the decrease in metabolism is after the ingestion of feed or how rapid the increase is due to feed ingestion. To study the influence of the ingestion of feed upon the carbon-dioxide production of an animal that has been fasting 24 hours, we have summarized in Table 56 such data as we have on this point, namely, for steers 3, 6, and 8. With the first two animals substantially a kilogram of hay was given after the standard metabolism had been measured, and following the ingestion of the hay the metabolism was again measured in consecutive half-hour periods for 1 to 2 or more hours. In the case of steer 3 the experiment began 11 minutes after giving feed, and in the case of steer 6 it began 14 minutes afterwards. Referring again to the computed values per 500 kg. of body-weight per half hour, we find that with steer 3 the ingestion of 1.13 kg. of hay resulted in an increase in the carbon-dioxide production from 55.5 to 59.9 grams, an increase of approximately 8 per cent. This exper-

iment fortunately was an ideal one, in that the animal exhibited remarkable muscular repose and the tests are not contaminated by differences in muscular activity. With steer 6, under exactly the same experimental conditions and with a very quiet series of 5 half-hour periods for the standard metabolism and 5 periods following the ingestion of 1.13 kg. of hay, we find no increase in the carbon-dioxide production. These two experiments by themselves have special interest in that the conclusion to be drawn from them would be that there is no measurable increase in metabolism during the first 2 or 2½ hours after the ingestion of about 1,000 grams of hay. That the metabolism does not increase during this time may be due to the fact that the hay must first be moistened and the cud rechewed, and that probably a considerable period of time elapses before the digestive juices have begun to work upon it and it has been resolved into soluble materials which can be absorbed and contribute to the metabolism of the animal. It should be pointed out here that the experiment with steer 6 complicates our interpretation of the activity records, since from the record of activities one would normally have expected in the post-feeding period with steer 6 an increase in the carbon-dioxide production, but instead there is a slight average decrease of 0.7 gram on the basis of per 500 kg. of body-weight.

As an index of the influence of full feed, i. e., a fattening ration, upon the carbon-dioxide production, a special test was made with steer 8 on July 16, consisting of 2 half-hour periods. This test showed that the carbon-dioxide production per 500 kg. of body-weight per half hour averaged 163.3 grams or somewhat more than 2½ times that of steers 3 and 6, which were measured under standard conditions and also after the ingestion of 1.13 kg. of hay. In considering this high carbon-dioxide value for steer 8 it must be recalled that this was obtained during a period of full feed and active digestion, with a very heavy ration, and during a period when there was undoubtedly formation of fat from the carbohydrate ingested. Under these conditions the carbon-dioxide to heat ratio is in all probability very different from that obtaining when fat is not being formed. Experimental evidence is very clear as to the calorific value of carbon dioxide and oxygen when the character of the combustion is either predominantly fat or carbohydrate, as expressed by the limits of the respiratory quotient of 0.70 and 1.00. Under the conditions of surfeit feeding carbohydrate is converted to fat, accompanied by the splitting off of a large amount of carbon dioxide, which has been designated as "atypical" carbon dioxide.[a] Just what is the true calorific value of 1 gram of carbon dioxide or oxygen under conditions where fat formation is taking place is not known. There is no experimental evidence on this point with direct calorimetry with which we are familiar. The Nutrition Laboratory has had this as a major problem for a number of years. A special calorimeter has been devised, the weight of which is not disproportionate to the weight of the animal studied, usually a goose or small pig, and a large number of experiments have been made on this point. The data are not yet ready for publication. It is clear, however, that in all problems of animal husbandry the matter of the formation of fat from carbohydrate is of greatest importance, for all rations pertaining to beef feeding, hog feeding, and milk production

[a] Bleibtreu, Arch. f. d. ges. Physiol., 1901, 85, p. 358.

are based upon the capacity of the animal to convert carbohydrate into fat. This problem of the calorific value of carbon dioxide and oxygen under conditions of formation of fat from carbohydrate assumes, therefore, a special significance. Accordingly, the fact that the excretion of carbon dioxide by steer 8 during full feeding was more than 2½ times the amount excreted by two other steers, which were fed small amounts of hay, does not represent the true mathematical ratio of the heat-production, for probably a not inconsiderable part of the carbon dioxide was of the atypical form.

For the special purpose of studying in a more detailed manner the influence of the ingestion of moderate amounts of feed, experiments were made with steers A and B during 1920, and these are recorded in Table 57. On January

TABLE 57.—*Carbon-dioxide production of steers A and B without feed for varying lengths of time.*

| Steer and date (1920). | Time of experiment. | Hours after feed. | Body-weight. | Average carbon-dioxide production per half hour. | | Activity. |
|---|---|---|---|---|---|---|
| | | | | Total. | Per 500 kg. | |
| | | *hrs.* | *kg.* | *gm.* | *gm.* | |
| Steer A Jan. 7 | 9h10m a. m. to 10h40m a. m. | [1]27 | 591 | 84.5 | 71.5 | III, III, III |
| Jan. 8 | 8 55 a. m. to 10 25 a. m. | 50 | 581 | 71.1 | 64.3 | III, III |
| Apr. 6–7 | 1 13 p. m. to 5 13 p. m. | [2]7 to 11 | [3]512 | 81.1 | 79.2 | II, II, II, III |
| | 5 13 p. m. to 9 13 p. m. | 11 15 | ..... | 80.2 | 78.3 | III, II, III, III |
| | 9 13 p. m. to 1 13 a. m. | 15 19 | ..... | 73.0 | 71.3 | III, III, III, II |
| | 1 13 a. m. to 4 15 a. m. | 19 22 | ..... | 69.3 | 67.7 | III, II, II |
| | 4 15 a. m. to 7 13 a. m. | 22 25 | ..... | 62.3 | 60.8 | II, III, II |
| | 7 13 a. m. to 10 13 a. m. | 25 28 | ..... | 68.8 | 67.2 | II, II, II |
| | 10 13 a. m. to 1 13 p. m. | 28 31 | ..... | 59.0 | 57.7 | II, II, II, III, II |
| Steer B Jan. 7 | 11 38 a. m. to 12 38 p. m. | [4]29 | 561 | 96.6 | 86.1 | II, II |
| Jan. 8 | 11 21 a. m. to 12 21 p. m. | 53 | 547 | 77.7 | 71.0 | I, II |

[1] Last feed received (4,545 gm. hay) was at 6h45m a. m., Jan. 6.
[2] Last feed received (2,000 gm. hay) was at 6h45m a. m., Apr. 6.
[3] Represents average of 516 kg. on Apr. 6 at 2 p. m., and 508 kg. on Apr. 7 at 2 p. m.
[4] Last feed received (4,545 gm. hay) was at 6h45m a. m., Jan. 6.

7, when steer A had been 27 hours without feed, his carbon-dioxide production per 500 kg. of body-weight per half hour was 71.5 grams, while on January 8, when he had been 50 hours without feed, it was 64.3 grams. Although the activity during this experiment was by no means as low as could be desired, this general lowering of the metabolism at the fiftieth hour is quite in line with the bulk of the evidence exhibited in Table 55. A more detailed test, however, was made on April 6 to 7, when the animal was fed 2,000 grams of hay about 6h45m a.m., April 6, and the metabolism was determined in several consecutive 3-hour to 4-hour periods until the thirty-first hour, the first period beginning 7 hours after the ingestion of feed. In this test the highest values are noticed at the beginning, with a distinct tendency for them to fall off until the thirty-first hour. While, therefore, we would consider from the data in Table 56 that little, if any, effect is to be noticed from the ingestion of hay for the first hour or two, the experiment of April 6 to 7 with steer A shows that between the seventh and eleventh hours after feed there is a rather high carbon-dioxide production, which has a distinct tendency to fall off as the fasting progresses, and the probabilities are that with this animal an average value of not far from 60 grams represents the standard carbon-

dioxide production per 500 kg. of body-weight per half hour at or about this time. This value of 60 grams is, as a matter of fact, a little higher than that found on other days near this date, possibly to be accounted for by the fact that during the experiment of April 6 to 7 steer A was continually confined inside the respiration chamber and had not been able to lie down at all for at least 23 hours before the last measurements were made, a condition which would introduce the element of exertion and fatigue.

With steer B a similar study was made on January 7 and 8, and in his case a pronounced decrease in the standard carbon-dioxide production per 500 kg. per half hour was noted at the fifty-third hour. No explanation for this decrease can be made on the basis of differences in muscular activity, and it would therefore appear as if with steer B at least we had to deal with a great reduction in the metabolic activity.

The difficulty of measuring the true basal metabolism has already been pointed out. We recognize, as was stated at the outset, that this experimental evidence concerning the influence of the ingestion of feed is very fragmentary and unsatisfactory. Nevertheless we believe our data show that although the metabolism of our steers under the conditions of these experiments was distinctly on a sliding scale, the fall in metabolism took place in large part by the twenty-fourth hour (although in a number of instances there was subsequently a still further decrease), and consequently our selection of a period 24 hours after the last feed for the measurement of the standard metabolism was in all probability as satisfactory as could be made. Another important conclusion to be drawn from this study is that with a feed made soluble with such difficulty as is hay and with the small amounts of feed allowed, we could in all probability have given our animals with perfect safety a moderate amount of feed just prior to the respiration experiments without affecting the standard metabolism for the next hour or two, thereby contributing to their general sense of euphoria and muscular repose and simultaneously increasing the accuracy of our measurements. This is a technical point that will bear further investigation as to its probable application in any subsequent tests of this nature.

Fortunately, much more satisfactory evidence with regard to the influence of fairly prolonged fasting upon the metabolism of ruminants has been supplied in unpublished data which Professor Armsby has kindly put in our hands, with the privilege of using them in connection with this report. In 1920 and 1921, Professor Armsby and his associates made experiments upon two fasting cows and determined directly the heat-production and the carbon-dioxide production throughout the entire time. Reference to these experiments has already been made in the discussion of our selection of the calorific value of carbon dioxide under different nutritive conditions. Professor Armsby's data show that for the first 24 hours beginning 24 hours after the withdrawal of feed, the heat-production of one of his cows was 6,814 calories and the carbon-dioxide production 2,208 grams. (See Table 66, p. 256.) During the second 24 hours the heat-production was 6,642 calories and the carbon-dioxide production 2,111 grams. With a second cow the heat production in the first 24 hours after 24 hours of fasting was 6,874 calories and in the second 24 hours 6,391 calories, while the carbon-dioxide production was 2,185 and 1,964 grams, respectively. Obviously, with neither of these animals

are the wide differences found that are found with several of our animals, as recorded in Table 55. The values reported by Professor Armsby are of course much more firmly established scientifically and undoubtedly more nearly represent the true case. As his complete data are not yet published, it is impossible to compare his records in detail with ours. Moreover, Professor Armsby's records of activity are not directly comparable with ours, as he did not employ graphic registration. In all probability the values obtained by him represent more strictly the sliding scale of metabolism with prolonged fasting, a scale which we have no reason to believe would be materially different from that noted with humans under similar conditions. Of vital importance is the fact that using the methane determinations as an index of digestive fermentations and intestinal digestive activity, Professor Armsby finds that the methane decreases very rapidly during the first 24 hours after the last feed and continues to decrease for the second 24 hours, with a very slight decrease thereafter until about the one hundred and eighth hour, when constancy seems to be established, the methane production at this time being very low, i. e., about 5 grams per 24 hours. This finding is quite in line with the early impression of Grouven[a] that the fill may continue to undergo fermentation and thereby contribute to the metabolism of the body for 3 or 4 days after the complete withdrawal of feed.

While, therefore, individual tests imply that the metabolism is somewhat lower after 48 hours of fasting than after 24 hours, we are quite inclined to think that, in view of many of our own tests, and particularly in view of the well-planned experiments of Professor Armsby, the selection of 24 hours after the withdrawal of feed was a particularly fortunate time for beginning our tests. Certainly in a differential method, where comparison is to be made of different animals at different times, this selection of time gives perfectly comparable results, provided we clearly bear in mind that we are not dealing either with complete muscular repose or the true post-absorptive condition, but with an arbitrarily specified condition, designated here as "standard metabolism."

### COMPARISON OF CARBON-DIOXIDE PRODUCTION OF STEERS WHILE STANDING AND LYING.

While having relatively little bearing upon the major points in our research, certain data have been obtained in specially designed experiments to throw further light, if possible, upon the rather unsettled problem as to the true increase in the metabolism of these heavy ruminants as a result of the change from the lying position to the standing position. Previous investigators differ rather widely in their findings. A special discussion of this matter is given by Von der Heide, Klein, and Zuntz,[b] who report a series of experiments (in which the tracheal-fistula method was employed) made by Klein upon the steer used in their large respiration chamber. In four periods in the morning, while the steer was standing without feed, the oxygen consumption on the average was 1,990 c. c. per minute and the carbon-dioxide production 1,605 c. c., with a respiratory quotient equal to 0.807. At night, when the steer was lying and sleeping, two periods showed an average oxygen consumption

[a] Grouven, loc. cit., p. 50.
[b] Von der Heide, Klein, and Zuntz, Landw. Jahrb., 1913, 44, p. 823.

of 1,639 c. c. and an average carbon-dioxide production of 1,359 c. c., with a respiratory quotient of 0.829. From these tests, which they consider especially satisfactory, the authors compute that with standing there is an increase in metabolism above that when lying and sleeping amounting to 20.7 per cent. Reference is made to the earlier work of Dahm[a] in Zuntz's laboratory, who found a considerably smaller increase due to standing, approximating 8 per cent. Finally, they compare the results obtained by Klein with those secured by Professor Armsby in his respiration calorimeter, and point out that the increase of 20.7 per cent found by Klein is much more nearly in accord with Armsby's slightly higher findings.[b]

It is impossible to make a large animal lie down in a closed respiration chamber. We had to design special experiments in which the animals were kept standing with a chain loosely stretched across the stanchions, so that they could not lower the head sufficiently to lie down. They were thus made to stand all day and then the chain was removed and the experimental period begun only after they had lain down voluntarily. These experiments were time-consuming, and because of the very extensive program which we had on hand, we could hardly make too heavy inroads upon our time. However, 7 series of comparisons were possible during the 2 years' work. These were occasionally complicated by the differences in activity when standing, but as a whole the comparisons seem fairly satisfactory. The results are recorded in Table 58 herewith. Although comparisons of this kind could not be made where weight differences were appreciable, for usually succeeding periods with the same animal were necessary, nevertheless, for the final purpose of analysis we have given the results on the basis of the carbon-dioxide production per 500 kg. of body-weight per half hour.

Of first importance in examining Table 58 is our evidence with regard to the uniformity in the carbon-dioxide production in periods while lying, and consequently each consecutive half-hour period is reported, so that we have a clear method of comparison. With steer 3 the first 3 periods in the lying position show a uniformity no better than the 3 periods in the standing position, although one would expect greater uniformity when lying than when standing. With steer 8 the results for the 2 periods when lying have a somewhat wider divergence than those for the 2 periods when standing, but in general the values are not far from the same. With steer 11, 4 periods when lying were available. Here the range is from 56.7 grams to 65.2 grams, a range far greater than that indicated in the 3 periods while standing, although it is to be noted that all 3 periods while standing were accompanied by considerable activity. With steer B, on September 15, 3 periods in the lying position show fairly close agreement, although the first and third periods were only 16 and 12½ minutes long, respectively, while the second was about 30 minutes long. The standing periods are much higher. On September 16, 3 consecutive periods lying (the last 2 of but 15 minutes' duration) show rather a wide range in the carbon-dioxide production per 500 kg. of body-weight per half hour, i. e., from 64.6 grams to 54.8 grams, although the last 2 periods show good agreement. Although 5 different periods were obtained with steer B on September 17, while lying, they were not consecutive. The animal

[a] Dahm, Biochem. Zeitschr., 1910, 28, p. 494.
[b] Armsby and Fries, Am. Journ. Physiol., 1913, 31, p. 245.

stood up and lay down intermittently and the technicians secured the best experimental periods possible, but even then it can be seen that there are very wide variations in the results, the values ranging between 56.0 grams and 80.6 grams, although this last value was for a period but 12 minutes long.

In general, therefore, the results during the consecutive or different lying periods are by no means so uniform as one would expect. If we compare lying periods obtained on different days, such as, for example, those with steer B, we find an extreme range in the carbon-dioxide production per 500 kg. of body-weight per half hour from a minimum of 54.8 grams on September

TABLE 58.—*Carbon-dioxide production of steers while standing and lying, 24 hours after feed.*

| Date and body-weight. | Steer No. and time of experiment.[1] | Position. | Carbon-dioxide production per 500 kg. per half hour. | | | | | | Activity. |
|---|---|---|---|---|---|---|---|---|---|
| | | | Period 1. | Period 2. | Period 3. | Period 4. | Period 5. | Average. | |
| | Steer 3. | | gm. | gm. | gm. | gm. | gm. | gm. | |
| Apr. 23 | 8h00m p. m. to 9h30m p. m. | Standing | 61.4 | 60.0 | 65.2 | ..... | ..... | 62.2 | I, I, II |
| 385 kg. | 9 55 p. m. to 11 20 p. m. | Lying[2] | 49.8 | 54.7 | 54.5 | ..... | ..... | 53.0 | I, I, I |
| May 1 | 8 04 p. m. to 9 34 p. m. | Standing | 57.0 | 58.3 | 57.7 | ..... | ..... | 57.7 | II, II, II |
| 387 kg. | 11 04 p. m. to 11 29 p. m. | Lying[3] | 53.9 | ..... | ..... | ..... | ..... | 53.9 | I |
| | Steer 8. | | | | | | | | |
| Oct. 22 | 8h41m a. m. to 10h11m a. m. | Standing | 72.3 | 66.5 | 64.4 | ..... | ..... | 67.8 | II, II, II |
| 552 kg. | 8 02 p. m. to 9 02 p. m. | Lying | 71.4 | 64.0 | ..... | ..... | ..... | 67.7 | ..... |
| | Steer 11. | | | | | | | | |
| Oct. 23 | 10h32m a. m. to 12h02m p. m. | Standing | 84.2 | 82.4 | 83.8 | ..... | ..... | 83.5 | III, III, III |
| 615 kg. | 8 09 p. m. to 10 30 p. m. | Lying | 60.7 | 65.2 | 63.8 | (4) | 56.7 | 61.6 | I, II, I, I |
| | Steer B. | | | | | | | | |
| Sept. 15 | 9h11m a. m. to 10h41m a. m. | Standing | 91.2 | 89.5 | 84.3 | ..... | ..... | 88.3 | I, I, I |
| 584 kg. | 12 01 p. m. to 4 54 p. m. | Lying | 78.7 | 72.4 | 76.0 | ..... | ..... | 75.7 | I, I, I |
| Sept. 16 | 9 12 a. m. to 10 42 a. m. | Standing | 75.3 | 87.0 | 77.9 | ..... | ..... | 80.1 | I, II, I |
| 570 kg.[5] | 11 13 a. m. to 12 56 p. m. | Lying | 64.6 | 55.2 | 54.8 | ..... | ..... | 58.2 | I, I, I |
| | 12 56 p. m. to 1 20 p. m. | Standing | 94.2 | ..... | ..... | ..... | ..... | 94.2 | ..... |
| | 1 21 p. m. to 1 50 p. m. | Lying | 64.9 | ..... | ..... | ..... | ..... | 64.9 | I |
| | 1 50 p. m. to 2 20 p. m. | Standing | 75.5 | ..... | ..... | ..... | ..... | 75.5 | ..... |
| Sept. 17 | 9 22 a. m. to 10 52 a. m. | Standing | 68.8 | 69.0 | 70.0 | ..... | ..... | 69.2 | I, I, I |
| 556 kg. | 11 19 a. m. to 4 15 p. m. | Lying[6] | 56.0 | 60.1 | 75.6 | 80.6 | 65.8 | 67.4 | I, I, I, I, I |

[1] Each period was approximately 30 min. long, except in 7 cases with steer B, when it was only about 15 min. long, i. e., periods 1 and 3, lying, on Sept. 15, periods 2 and 3, lying, on Sept. 16, and periods 3, 4, and 5, lying, on Sept. 17.

[2] Steer lay down at 9h50m p. m.; stood up 1 minute before end of last period; previous to experiment had been made to stand all day.

[3] Steer had been made to stand all day previous to experiment; was very restless between 9h34m and 10h58m p. m; lay down at 10h58m p. m.

[4] Steer stood up and lay down again in this period.

[5] Average of body-weights on Sept. 15 and 17; steer not weighed on Sept. 16.

[6] These lying periods were not consecutive; all other periods were consecutive.

16, in the third lying period, to a maximum of 80.6 grams on September 17, in the fourth lying period. Since the opportunity for muscular activity is much reduced when the animal is lying, and since we have already seen that intense muscular activity can of itself rarely increase the metabolism more than 25 per cent, it is quite clear that we have here, even in the lying position, two distinctly different metabolic levels represented by these two extreme figures. This is all the more reason, then, for insisting that in experiments of this type only consecutive periods or nearly consecutive periods should be compared, and that the standing periods should preferably first precede the lying periods and subsequently follow the lying periods. This condition was met only in the experiment of September 16 with steer B. Here the carbon-dioxide production per 500 kg. of body-weight per half hour for the first 3

consecutive periods lying was 58.2 grams on the average and for the later single period lying 64.9 grams. When steer B was standing, the first 3 consecutive periods gave an average of 80.1 grams, while 2 succeeding periods gave values of 94.2 grams and 75.5 grams, respectively. Here the disagreement between the different periods is such that an intelligent comparison of the true effect of standing over lying is entirely out of the question. On September 17 the average for the 3 standing periods with steer B was 69.2 grams and the average for the 5 isolated lying periods was 67.4 grams, or nearly the same. With steer 8, likewise, on October 22, there was practically no difference in the carbon-dioxide production, whether the animal was standing or lying. The fact, however, that in 3 cases (steer 3 on April 23 and May 1, and steer B on September 15) lower values were found when the animal was lying than when he was standing, even though the muscular activity was the same in both positions, leads to the belief that the increase in metabolism due to standing under the conditions of our experiments is not far from 17 per cent.

We are by no means satisfied with the results of these tests. They were made in connection with other observations and under conditions that can hardly be considered ideal. Unfortunately, they do not contribute greatly to our knowledge with regard to the difference in metabolism when the steer is lying and standing. Until a uniform series of periods in the standing position can be secured with a similar uniform series of periods in the lying position immediately following it, there is little opportunity for definite deductions. Probably these conditions just outlined are best fulfilled by the first experiment with steer 3 and by the first experiment with steer B. The experiment with steer 11 would be ruled out on account of the excessive activity during the standing periods, which resulted in abnormally high values. With steer 3, on April 23, the increment in metabolism due to standing is about 17 per cent and with steer B, on September 15, the increment is also about 17 per cent. This increment is not far from the increase of 20 per cent noted in the later observations of Zuntz and his associates.

### INFLUENCE OF ENVIRONMENTAL TEMPERATURE.

Based upon the conception that a warm body will lose heat more rapidly to a cold environmental temperature than it will to an environmental temperature nearer its own, statements exist commonly in all treatises on animal physiology to the effect that more feed is needed with the lower environmental temperature. A typical statement is that by Kellner[a] to the effect that "the lower the stall temperature the greater is the heat lost by the animal through radiation and conduction, and therefore more feed must be given." This statement is in large part based upon practical feeding tests and upon certain experimental data accumulated on small animals. Little, if any, evidence is available from experiments on ruminants. In our own series of tests, special effort was made to have the environmental temperature inside the respiration chamber as constant as possible. Electric heaters were used primarily for this purpose. As a matter of fact, the environmental temperature did range in our experiments from as low as 3° C. to as high as 28° or 30° C. The majority of our experiments, however, were made at a tempera-

[a] Kellner, Die Ernährung der landw. Nutztiere, Berlin, 1920, 9th ed., p. 448.

ture not far from 16° to 20° C. We have inspected all of our data most carefully, comparing different periods at different temperatures with the same animal, taking into consideration activity, nutritive plane, and stage of digestion, and we fail to find (within the temperature limits in which we worked) any uniformity whatsoever in the relationship between the metabolism and the environmental temperature. (See, also, p. 301 for further discussion of this point.) In this finding we are in accord with the opinion of Armsby that "apparently the critical temperature of ruminants is rather low."[a] In many States it is the common practice to compare steers fed under protected and unprotected conditions, but the evidence is conflicting as yet as to the real necessity for larger amounts of feed when the animals are exposed.

Certain data in our series suggest so strongly, however, that the metabolism is lower the lower the temperature, that a definite series of experiments on the influence of the environmental temperature on the standard metabolism of ruminants is now in progress in the respiration chamber at Durham.

## Theoretical Considerations on the Physiological Comparison of Animals.

### COMPARISON ON THE BASIS OF LIVE BODY-WEIGHT.

In all physiological research it is important to compare frequently different animals of the same species and not infrequently different animals of different species, and finally, of even greater interest to us, to compare the same animal at several states of nutrition. For purposes of comparison, the most obvious, simplest, and earliest method was that on the basis of mass. A large animal would eat more food, would have greater respiratory activity, and produce more heat than a small animal. This method of comparing animals per unit of weight, either pound or kilogram, has been very extensively used. Thus, it is the common custom in many German institutions to figure rations for live stock on the basis of a given weight, usually 1,000 kg. of live body-weight, and in America on the basis of 1,000 pounds or 500 kg. of live body-weight, the two latter standards representing an attempt to secure a uniformity of weight by using as a standard an animal weighing on the average not far from the average weight of adult steers and horses. Kellner's[b] computation of the normal ration for different animals is based entirely upon the requirements per 1,000 kg. of body-weight per day. On the other hand, practically all American computations are based upon the needs per 1,000 pounds, a procedure which is somewhat more logical, since it more nearly represents the average weight of adult horses and cattle.

This method of comparison obviously makes the very erroneous assumption that each kilogram or each unit of body-mass has exactly the same heat-producing capacity. This assumption is particularly erroneous when one is dealing with beef animals, where large amounts of inert fat may be an important part of the total body-weight. Thus, in comparing two animals, one with a weight of 500 kg. and the other with a weight of 400 kg., the proportion of fat, flesh, and bone may be essentially the same and the difference in weight may simply represent a different stage of growth, one animal being older

[a] Armsby, The nutrition of farm animals, New York, 1917, p. 312.
[b] Kellner, Die Ernährung der landw. Nutztiere, Berlin, 1920, 9th ed., p. 650.

than the other, or a difference in race, one being smaller than the other, but both of the same age. The situation is even more complicated, however, when the attempt is made to compare the same animal under two different conditions of body-weight. Here we may have two distinct conditions for comparison; first, that represented by difference in age, when the animal weighs 400 kg. and later weighs 500 kg., weights representing normal growth and development in which the proportion between fat, flesh, and bone may not be materially different in the two cases; and second, that condition where the difference in age is less important, when differences in the animal's weight are due to excessive fattening or to withdrawal of feed and the changes in body-weight occur rapidly. The situation is very different in the second condition, since with the lighter-weight animal there is a relatively larger proportion of flesh and bone and a much smaller proportion of fat, the latter having been drawn upon as a result of the undernutrition. The body-weight basis, however, is very extensively used and does furnish a quick, easily comprehensible basis for comparing two animals of not greatly unlike weight or for comparing the same animal under two different conditions when there are not marked differences in its body-weight. We believe that the 500-kg. basis serves the dual purpose of retaining the metric unit and bringing all animals to an average weight not far from that of the normal adult steer. Consequently, in the report of our experiments in many of the tables the values have been computed per 500 kg. of body-weight.

### COMPARISON ON THE BASIS OF BODY-SURFACE.

A unit of reference in many comparative researches is the surface-area of the body, based primarily upon the assumption that heat-production is proportionate not to body-weight but body-surface, from which heat is lost to the environment. The history and development of the so-called "body-surface law" has received extended discussion by Harris and Benedict.[a] More attention has been given to the development of this "law" in connection with experiments on humans than perhaps on any other species, and yet the earliest interest was manifested by workers in animal physiology. Indeed, we find specific attention given to this matter as early as 1864 by Grouven, who, doubtless influenced by the previous considerations of Rameaux,[b] Thillaye,[c] and Bergmann,[d] considered that the animal should be compared on the basis of surface-area and not on the basis of body-weight. Arguing from the similarity of geometrical solids, Grouven made comparisons between his steers, using the two-thirds power of the body-weight as indicative of the ratio which two like geometrical solids of different mass but equal density bear to each other.[e] It is to be observed that he made no attempt to measure or,

[a] Harris and Benedict, Carnegie Inst. Wash. Pub. No. 279, 1919, pp. 129 et seq.

[b] Sarrus and Rameaux, Compt. Rend. Acad. Sci., Paris, 1838, **6**, p. 338; loc. cit., 1839, **9**, p. 275. See, also, Rameaux, Bull. Acad. roy. d. sci. de Bruxelles, 1839, **6**, (2), p. 121; *ibid.*, Mém. couron. Acad. roy. d. sci. (etc.) de Belg., Brux., 1858, **39**, 64 pp.

[c] Robiquet and Thillaye, Bull. Acad. roy. de Méd., Paris, 1839, **3**, p. 1094.

[d] Bergmann and Leuckart, Anatomisch-physiologische Übersicht des Thierreichs, Stuttgart, 1852; see especially p. 272. Also Bergmann, Ueber die Verhältnisse der Wärmeökonomie der Thiere zu ihrer Grösse, Göttingen, 1848. An earlier paper in Müller's Archiv, 1845, p. 300, is also cited.

[e] Grouven, loc. cit., pp. 155, 156, 161, and 162.

indeed, to compute the body-surface, his method of relative comparison being simply to use the two-thirds power of the body-weight of the animals to be compared. With the development of the Meeh formula[a] for computing the surface-area of man, using the two-thirds power of the body-weight and applying a factor supposed to be determined by actual measurement to secure true surface-areas, similar procedures were made with regard to some of the domestic animals. Thus, while with mankind the two-thirds power of the body-weight was multiplied by the factor 12.312, with a horse Hecker[b] used the factor 9.02. This method for calculating the energy requirements per unit of surface-area was resorted to relatively little, however, and the live weight has for many years remained as a basis for comparing the energy needs of large domestic animals. Even in so recently reported experiments as those made with the new respiration chamber by Zuntz, Von der Heide, and Klein,[c] the comparison is made on the basis of 1,000 kg. of body-weight.

In America, Professor Armsby has consistently taken the ground that comparisons should not be made on the basis of the body-weight, but on the basis of the two-thirds power of the body-weight. Two decades ago, in making his first report upon experiments with the respiration calorimeter, Armsby specifically stated that the computations are best made on the basis of 500 kg. of live weight, "on the assumption that the maintenance requirement is proportional to the two-thirds power of the live weight."[d] Thus he restored and put into active practice the plan of Grouven. It was many years before the specific idea of measuring body-surface accurately stimulated the accumulation of direct experimental evidence, and our thanks are due to the investigators at the Missouri Agricultural Experiment Station, primarily to Professor C. R. Moulton and his associates, for attempting to correlate body-weight and measured skin-area by means of most careful records.

In a special report on his investigations, Moulton[e] compares the actually observed values of surface-area and body-weight in 35 steers, and since the specific gravity of like animals is about constant, the general formula $S = KW^{\frac{2}{3}}$ (where $S$ is the surface-area and $W$ the body-weight) is the starting-point of the investigation. In the experimental treatment of the matter, Moulton points out the very significant fact that the use of live weight itself is erroneous, since a considerable part of the live weight is "fill," which has a very variable mass. He accordingly measured the warm empty weight, i. e., live weight less contents of stomach and intestinal tract, and actually measured the hide, then comparing the relationship between the two measurements and deriving a factor, $K$. He found that this factor varied greatly with different animals, ranging from 7.32 to 10.48, according to the fatness of the animal. Moulton's steers were divided into three groups, Group III representing very thin animals, for which the factor averaged 9.92. Group II represented medium thin animals, which were fed for maximum growth without the laying on of appreciable fat, and for this group the average factor was 9.37. The

[a] Meeh, Zeitschr. f. Biol., 1879, 15, p. 425.
[b] Hecker, Zeitschr. f. Veterinärk., 1894, 6. Jhrg., p. 97; cited by Armsby, Principles of animal nutrition, New York, 1906, 2nd ed., p. 364.
[c] Von der Heide, Klein, and Zuntz, Landw. Jahrb., 1913, 44, p. 829.
[d] Armsby, Bureau Animal Industry, Bulletin 51, 1903, p. 63.
[e] Moulton, Journ. Biol. Chem., 1916, 24, pp. 303 et seq.

animals in Group I were full-fed from birth, and in this group the younger animals gave an average value for $K$ of about 8.57, as compared with 7.65 found with the older animals.

As a result of his careful analysis, Moulton finds that for cattle in thin or medium condition the relationship between body-surface and body-weight is represented better by the five-eighths power of the weight, and for fat cattle by the five-ninths power, than by the conventionally accepted two-thirds power. Moulton's corrected formulæ are given by Armsby, Fries, and Braman as follows:[a]

For cattle in thin or medium condition, $S = 0.1186\ W^{\frac{5}{8}}$
For fat cattle, $S = 0.158\ W^{\frac{5}{9}}$

Here $W$ equals the empty weight in kilograms and $S$ the body-surface in square meters. These formulæ, it is seen, derive the surface-area from the empty weight and do not bring in the varying value of $K$.

We are further indebted to Moulton[b] for estimates as to the probable warm empty weights (i. e., live weights less "fill") of animals under different conditions of feeding. Thus, he finds that the average percentage of empty weight with Group III, cattle over 1 year old, is 88.9. With the cattle in Group II, more than 1 year old, the average value is 89.5 per cent, while with the special, full-fed animals it is approximately 92 per cent. From these figures one may compute, as we have in our own data, the probable warm empty weight and, by difference, the probable weight of fill. Consideration of actual computations in the case of our own individual animals will show the errors that are liable to creep into such estimates of body-surface. The important point to be noted here is that the body-weight alone gives an approximate measure for comparison and that the two-thirds power of the body-weight gives possibly a somewhat closer estimate. When fill can be accurately determined, as in slaughter tests, the consideration of the warm empty weight rather than the total weight is an experimental step certainly in the right direction. Moulton's most careful computation of the body-surface from the measured constants is a degree of refinement that is theoretically an advancement in method, but can not as yet be considered as being closely representative of the actual physiological facts bearing upon heat-loss.

### Method of Estimating the Surface Area of Steers at Different Stages of Nutrition.

Most of the comparisons made in this report have to deal primarily with the same animal at different stages of nutrition. On the other hand, a group of steers, Nos. 2, 4, and 5, were specially held as normals and controls, and direct comparison with them is important. It is admitted that when comparing the control animals with their normal proportions of fat, muscle, and bone, with the other animals whose store of fat and protein was greatly depleted, the method of using the live weight directly or any power of the live weight as a basis of computation may be fairly challenged. We have used the body-weight, but realize that it must be used with reservations. In lieu of any more accurate measure of the active metabolic tissue in these animals, and in an effort to secure every conceivable legitimate method of comparison, we have

[a] Armsby, Fries, and Braman, Journ. Agric. Research, 1918, 13, p. 47.
[b] Trowbridge, Moulton, and Haigh, Univ. Missouri, Agric. Expt. Sta., Bull. 18, 1915, pp. 11 and 41.

computed the metabolism per square meter of body-surface per 24 hours, making extensive use of the Moulton formulæ and constants. The formulæ require, first, the application of the probable percentage of warm, empty weight to live weight. This percentage varies, as is shown by Moulton's figures, with an extreme range of from 83.2 per cent to 94.3 per cent, but both of these extremes are with animals under 1 year of age. Considering only steers 2 years old or over, we find on reference to Moulton's data[a] a minimum of 85.4 per cent with steer 590, 3 years 1 month old, and a maximum of 94.2 per cent with an exceedingly fat "show" animal. The *average* values range, as stated before, from 89 to 92 per cent, which is a relatively small variation. To apply these values to other cattle involves, in the first place, an estimate

TABLE 59.—*Condition of steers during the observations and estimated percentage of empty weight, based on condition.*

| Group and steer No. | Age at beginning of observation. | | Dec. 22, 1918.[1] | | Feb. 7, 1919.[1] | | May 5, 1919.[1] | | Aug. 26, 1919. | | Nov. 3, 1919. | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | Condition. | Empty weight. | Condition. | Empty weight. | Condition. | Empty weight. | Condition. | Empty weight. | Condition. | Empty weight. |
| Group I: | *yrs.* | *mos.* | | *p. ct.* | | *p. ct.* | | *p. ct.* | | *p. ct.* | | *p. ct.* |
| Steer No. 2 | 2 | 8 | M− | 89 | M− | 89 | M− | 89 | M+ | 90 | ..... | ..... |
| Steer No. 4 | 3 | 8 | M− | 89 | M− | 89 | M− | 89 | F − | 91 | ..... | ..... |
| Steer No. 5 | 4 | 8 | M− | 89 | M− | 89 | M− | 89 | F − | 91 | ..... | ..... |
| Group II: | | | | | | | | | | | | |
| Steer No. 1 | 4 | 8 | T + | 88 | T − | 87 | E − | 85 | M− | 89 | F − | 91 |
| Steer No. 3 | 3 | 8 | M− | 89 | T + | 88 | E + | 86 | M+ | 90 | F − | 91 |
| Steer No. 7 | 2 | 8 | M− | 89 | T + | 88 | E + | 86 | M+ | 90 | F − | 91 |
| Steer No. 10 | 5+ | | M− | 89 | T − | 87 | E + | 86 | M− | 89 | F − | 91 |
| Steer No. 11 | 3 | 8 | M− | 89 | T + | 88 | E + | 86 | M+ | 90 | F − | 91 |
| Group III: | | | | | | | | | | | | |
| Steer No. 6 | 2 | 8 | T + | 88 | T − | 87 | E − | 85 | T + | 88 | T + | 88 |
| Steer No. 8 | 3 | 8 | M− | 89 | T − | 87 | E − | 85 | M+ | 90 | F + | 92 |
| Steer No. 9 | 5+ | | T − | 87 | T − | 87 | E − | 84 | E − | 85 | E + | 86 |
| Steer No. 12 | 2 | 5 | T − | 87 | E + | 86 | E − | 84 | M− | 89 | M− | 89 |
| Group IV: | | | | | | | | | | | | |
| Steer A | 3 | 8 | M− | 89 | E + | 86 | M+ | 90 | ..... | ..... | ..... | ..... |
| Steer B..... | 3 | 8 | M− | 89 | E + | 86 | M+ | 90 | ..... | ..... | ..... | ..... |

[1] For Group IV the dates were Jan. 2, May 29, and Dec. 26, 1920, respectively.

as to their general condition, i. e., as to whether they are thin, moderately thin, fat, or very fat, and in our particular case involves estimates of the general condition of our animals at different nutritive planes.

Our animals were carefully judged as to general condition on several dates, the first three groups of 12 steers being judged on December 22, 1918, and February 7, May 5, August 26, and November 3, 1919, while steers A and B were judged on January 2, May 29, and December 26, 1920. In Table 59 are given the results of the scoring of these animals on these dates, as to whether they were in a fat (F), medium (M), thin (T), or emaciated (E) condition, a plus and minus scale being allowed under each head.

Since our animals, in view of their prolonged submaintenance rations, probably underwent a greater change in condition of flesh than most of the animals considered by Moulton, we have extrapolated his percentages of empty weight, making use of some of his individual values for his very thin,

[a] Trowbridge, Moulton, and Haigh, Univ. Missouri, Agric. Expt. Sta., Bull. 18, 1915, Table 2, pp. 9 and 10.

mature animals, and have made an arbitrary division of his values as follows: F+, 92 per cent; F−, 91 per cent; M+, 90 per cent; M−, 89 per cent; T+, 88 per cent; T−, 87 per cent; E+, 86 per cent; and E−, 85 per cent and below.

A consideration of Moulton's data shows that two methods for estimating the body-surface area may be employed. Both methods use certain constants in common, such as, for example, the relationship between the warm empty weight and the live weight. One method employs a fluctuating value of $K$ in the general formula $S = KW^{\frac{2}{3}}$. The simpler formula suggested by Moulton, in which the five-eighths power of the empty weight is taken into consideration, employs for thin and moderately thin animals a constant 0.1186. While we have used this latter formula in computing the surface-areas of our steers, it is of considerable interest to note the pitfalls that are present in these methods of computation, particularly in that method where the value of $K$ is applied to the two-thirds power of the empty weight. In both of Moulton's methods the condition of the animal, as to whether it is excessively fat or excessively thin, plays rather a large rôle. His factor $K$ varies considerably with the condition of the animal, but since none of our animals went beyond the fat stage, we have to deal actually with percentages ranging only from 85 and below to 92. On this basis we have interpolated Moulton's factors for $K$ as follows:

| Per cent empty weight | 92 | 91 | 90 | 89 | 88 | 87 | 86 | 85 and below |
|---|---|---|---|---|---|---|---|---|
| Factor for $K$ | 7.65 | 7.65 | 8.40 | 9.50 | 9.62 | 9.75 | 9.87 | 10.00 |

Our first method of computing the surface-area involved the use of Moulton's constants for the percentage of live weight, as given by us on page 223 and the application of the values for $K$, as given above, to the two-thirds power of the empty weight. This method presented no particular difficulty with animals during the period of submaintenance. It was only in the realimentation period that we began to find an abnormal situation. Based upon the physical condition, as estimated on the several dates (see Table 59, p. 223), we would expect to use with these animals a continually decreasing factor for $K$ as the animal grows fatter and approaches the stage for marketing. For one of the steers which presented wide variations in body-weight, i. e., steer 1, we have computed the surface-areas by the formula $S = KW^{\frac{2}{3}}$ and also by the formula $S = 0.1186W^{\frac{2}{3}}$, as shown in Table 60. Down to June 24 the factor for $K$ was, as a rule, held at 9.75, except for the period of low weights from April 8 to May 14, when it was taken as 10.00. After June 24 the factor for $K$ would become less and less, in accordance with the increasing fatness of the animal, arriving finally at the low value of 7.65 at the end of the experiment. But if we compute the surface-area by the use of these factors, we come upon the anomalous situation that on October 29, 1919, steer 1, with a body-weight of 691 kg., has a computed body-surface of 5.62 square meters, as compared with a computed body-surface of 6.15 square meters on December 7, 1918, when he weighed over 100 kg. less. The fact that animals may have essentially the same weight and yet have markedly different surface-areas was strikingly shown by Moulton in his original series of measurements,[a] in the case of two adult steers, Nos. 512 and 121. No. 512 was 4 years

[a] Trowbridge, Moulton, and Haigh, Univ. Missouri, Agric. Expt. Sta., Bull. 18, 1915, Table 4, p. 14.

old and belonged to the second group, which was fed for maximum growth without the laying on of appreciable fat. His warm empty weight was 493.9 kg. and his surface-area was 6.01 square meters. No. 121 was 3 years old and belonged to the first group of fat steers. He had only a slightly greater empty weight than No. 512, namely, 508.5 kg., but his surface area was 5.01 square meters.[a] In view of this fact it is probably not surprising that there may be an increase in body-weight and a decrease in body-surface, but with our animal, steer 1, it is hardly to be considered that an increase in weight of 110 kg. or about 20 per cent could be accompanied by a *decrease* in surface-area of about 10 per cent.

TABLE 60.—*Body-surface of steer 1, computed by two different methods.*

| Date. | Live weight. | Per cent of live weight. | Empty weight ($W$). | Factor for $K$. | Body-surface. | |
|---|---|---|---|---|---|---|
| | | | | | $S=KW^{\frac{2}{3}}$. | $S=0.1186W^{\frac{5}{8}}$. |
| 1918–19. | *kg.* | | *kg.* | | *sq. m.* | *sq. m.* |
| Dec. 7 | 581 | 88 | 511 | 9.62 | 6.15 | 5.85 |
| Jan. 10 | 517 | 87 | 450 | 9.75 | 5.73 | 5.40 |
| Jan. 16 | 507 | 87 | 441 | 9.75 | 5.65 | 5.33 |
| Jan. 24 | 514 | 87 | 447 | 9.75 | 5.70 | 5.38 |
| Jan. 30 | 499 | 87 | 434 | 9.75 | 5.59 | 5.28 |
| Feb. 12 | 501 | 87 | 436 | 9.75 | 5.61 | 5.31 |
| Feb. 21 | 496 | 87 | 432 | 9.75 | 5.57 | 5.26 |
| Feb. 27 | 491 | 87 | 427 | 9.75 | 5.53 | 5.23 |
| Mar. 7 | 484 | 86 | 416 | 9.87 | 5.50 | 5.14 |
| Mar. 17 | 483 | 86 | 415 | 9.87 | 5.49 | 5.13 |
| Apr. 8 | 469 | 85 | 399 | 10.00 | 5.42 | 5.01 |
| Apr. 16 | 454 | 85 | 386 | 10.00 | 5.30 | 4.91 |
| Apr. 28 | 461 | 85 | 392 | 10.00 | 5.36 | 4.95 |
| May 5 | 454 | 85 | 386 | 10.00 | 5.30 | 4.91 |
| May 14 | 478 | 85 | 406 | 10.00 | 5.48 | 5.06 |
| May 20 | 505 | 87 | 439 | 9.75 | 5.63 | 5.32 |
| May 26 | 497 | 87 | 432 | 9.75 | 5.57 | 5.26 |
| June 3 | 486 | 87 | 423 | 9.75 | 5.49 | 5.19 |
| June 10 | 499 | 87 | 434 | 9.75 | 5.59 | 5.28 |
| June 19 | 511 | 87 | 445 | 9.75 | 5.68 | 5.36 |
| June 24 | 520 | 87 | 452 | 9.75 | 5.74 | 5.41 |
| June 30 | 542 | 88 | 477 | 9.62 | 5.87 | 5.60 |
| July 11 | 555 | 88 | 488 | 9.62 | 5.96 | 5.68 |
| Sept. 6 | 637 | 89 | 567 | 9.50 | 6.51 | 6.24 |
| Sept. 17 | 653 | 90 | 588 | 8.40 | 5.90 | 6.38 |
| Oct. 21 | 682 | 91 | 621 | 7.65 | 5.57 | 6.60 |
| Oct. 29 | 691 | 91 | 629 | 7.65 | 5.62 | 6.66 |

A comparison between this method of computing body-surface and that employing the formula $S=0.1186W^{\frac{5}{8}}$ is strikingly made in the last two columns for body-surface in Table 60, and it can be seen that the inconsistency pointed out above, namely, an increase in body-weight accompanied by a decrease in surface-area, does not occur when the body-surface is derived from the five-eighths power of the empty weight multiplied by the factor 0.1186. Accordingly, in all of our tables we have computed the surface-area from the latter formula, $S=0.1186W^{\frac{5}{8}}$.

[a] Unfortunately, Moulton's data published in 1915 do not give the lengths or photographs of either animal for comparison at the time of slaughter, although measurements of No. 512 are recorded at a later date (Univ. Missouri, Agric. Expt. Sta., Bull. 43, 1921, pp. 90 and 91).

One has but to examine the photographs of animals at different stages of nutrition to note that the conditions at two different dates do not represent like geometrical figures, and it is unquestionably true that the specific gravity could not be the same under the varying conditions. Chest circumferences indicate very considerable increases in the surface-area, increases not at all measurable by the changing factors of $K$, as suggested by Moulton. Admittedly the whole procedure for estimating surface-area is still in an experimental stage, and many of the assumptions are debatable and may fairly be challenged. The formulæ do, however, represent a serious attempt to secure some method which will allow, first, a comparison of the same steer under different nutritive conditions, and second, a comparison of different groups of steers in various states of flesh with a group of normal steers. When it is considered that the amount of fill in an adult steer may equal 10 per cent of his body-weight and may vary with the percentage of crude fiber in the feed, and finally that this fill, if computed as part of the live body-weight, is commonly figured into the active body-mass producing heat, the errors involved are obvious. Attempts have been made repeatedly to show that all warm-blooded animals have essentially the same heat-production per unit of surface-area, and to this end the fasting, carnivorous animal, the dog, has frequently been compared with the full-fed, fill-retaining ruminant, 10 per cent of whose body-weight may be intestinal ballast or fill, which plays only a slight rôle by fermentation in the heat-production. Such a comparison is of great physiological importance, for while it is obvious that a smaller animal or an animal reduced in weight by starvation would have a lessened heat-output, it is very important to know whether the animal in the reduced condition has a larger heat-output per unit of mass or per unit of surface-area or, what is even still more desirable but unfortunately as yet unattainable, per unit of active protoplasmic mass. It is for this purpose that the several comparisons are made in the subsequent discussion.

### Tests of Photographic Method for Determining Body-surface.

The remarkable agreement between the body-surface of the nude human body when determined by the measurement of certain anatomical photographs and when actually measured by the Du Bois linear formula[a] led to the hope that a photographic method for estimating the surface-area of animals could be used. Profile photographs of humans, taken against a white screen, showing a standing posture with the left arm extended and a meter-stick placed along the median line of the back to allow measurements, gave a simple method of measuring with a planimeter the surface-area of the body. Thus, the surface-area of the body was computed by referring the planimetered area of the profile photograph to the square of the photographic length of the meter-stick. It was found that if the planimetered area was multiplied by the factor 5.02, the result would represent the true surface-area, even with extraordinary variations in physical configuration of both men and women. This profile view is not unlike that taken anatomically of the side of an animal, the animal's legs representing the leg and arm of the human. Consequently, in taking photographs of our animals at different times of the year, a stick, 2 meters long, was suspended above the backbone of

[a] Benedict, Am. Journ. Physiol., 1916, 41, p. 275.

the animal so as to be included in the photograph. The treatment of these photographs by the method employed with humans, i. e., using the planimetered area and the actual photographic length of the meter-stick, gives values for surface-area (when multiplied by the factor 5.02 obtained for humans), that are so far in discord with the measured surface-areas reported by Moulton that we feel this photographic method has no value. Thus, in the typical case of steer 9, on June 7, the profile photograph corresponds to a side area of 1.8755 square meters. This multiplied by the factor 5.02, gives a total area of 9.415 square meters. The actual body-surface obtained by use of Moulton's formula is but 5.01 square meters. In this particular case we can see that instead of using 5.02 as the constant, we might assume that the photograph represents a series of cylinders, use the constant $\pi$, and more nearly approximate the true body-surface. Since, however, this selection of a factor to fit the areas computed by the Moulton formula would simply be referring all measurements to the Moulton constants, it is obviously not an improvement of his method, but, in fact, an unnecessary complication. Had there been an agreement between the constant found for humans and that found for animals, the situation would have been markedly bettered, for such agreement could hardly have been considered as merely fortuitous.

### Method of Presenting the Gaseous Metabolism Data.

Our intense physiological study of several groups of animals, extending practically throughout two years and involving respiration experiments, records of body-weight and pulse-rate, and determinations of the metabolizable energy of feed, etc., resulted in an accumulation of data, the presentation of which in a concise, comprehensive form is somewhat difficult. Certain of the data have already been treated in the foregoing sections, but the most important single feature of our work, the measurement of the gaseous metabolism and the energy transformations computed therefrom, still remains to be discussed.

The metabolism experiments with our 14 steers number usually not far from 25 with each animal. On each day that the animal was in the respiration chamber the carbon-dioxide production was measured usually in three half-hour periods, occasionally two, and rarely one. Space does not permit the recording of the values for each individual period inside the respiration chamber, but we may state that the agreement was reasonably satisfactory in all cases, very widely diverging periods being occasionally omitted from the average when they were obviously outside of the experimental series. In addition to the measurement of the carbon-dioxide production, we likewise measured the pulse-rate, and from the carbon-dioxide production have computed not only the total 24-hour caloric output, but also the heat-production per 500 kg. of body-weight, and per square meter of body-surface per 24 hours. The tabular presentation of the data (see Tables 62 to 80) includes the live weight recorded on the day of the experiment, the estimated percentage of empty weight ($W$) to live weight, the body-surface as computed by Moulton's formula, $S=0.1186W^{\frac{2}{3}}$, the number of half-hour periods involved in the gaseous-metabolism measurements, the average temperature of the chamber (recorded primarily to indicate more closely the exact conditions of the experiment), the average carbon-dioxide production as actually measured

per half hour[a] (from which is computed the total 24-hour heat-production and the heat-production per 500 kg. of body-weight and per square meter of body-surface per 24 hours), and the average pulse-rate per minute during the week nearest to the date of the respiration experiment.

In addition to the several tables, we have prepared a series of charts (see Figs. 25 to 27, 30 to 38, 41 and 42) upon which all these data are graphically recorded, so that for each animal one can compare the changes in body-weight, pulse-rate, carbon-dioxide production, and computed heat-production. In general, the data given in the several individual tables are those used for plotting the charts. Two exceptions, however, must be noted. In the first place, the body-weights in the tables are those actually obtaining on the days of the respiration experiments, and these body-weights were used for computing the body-surface and the heat-production per 500 kg. of body-weight and per square meter of body-surface. The body-weights plotted on the charts, however, represent the averages of 7-day periods. In the second place, the pulse-rates recorded in the tables represent average values for the week in which the respiration experiment occurred, while in the charts the average pulse-rates for every week throughout the year are plotted, just as in the case of the body-weights. In computing the average weekly pulse-rates, records secured when the steer was eating or ruminating were not included, and no week's average was plotted unless there were at least three days from which to draw the average.

The method for computing the body-surface by Moulton's formula has already been discussed in detail (see p. 222), and it is necessary only to point out again here that, in the formula $S = 0.1186W^{\frac{5}{6}}$, $W$ represents not live weight but the empty weight computed by multiplying the live weight by the percentage of empty weight to live weight. The metabolism measurements here recorded are not measurements of *basal* metabolism, for although they were made 24 hours after the last feed, we have reason to believe, from the experience of Grouven and the recent experience of Armsby, that there is some absorption of food material from the alimentary tract even after 24 hours. Secondly, the measurements were not made during complete muscular repose, for the animals were standing and not lying, thereby sustaining a heavy weight (so that there could not have been muscular relaxation as the word "repose" implies), and there was rarely complete absence of muscular movements. But the measurements do represent what we have selected as *standard* conditions, suitable for comparative purposes, namely, at a period probably somewhat later than the most active digestion and with the reasonably uniform muscular activity of standing quietly in a stall.

In considering these tables and charts it should be remembered that steers 1 to 12 (i. e., Groups I, II, and III) were treated experimentally in the same chronological period, but that steers A and B (Group IV) were studied a year later, and that the ration curtailment for Groups II and III began on December 22 and for Group IV on January 10. Horizontal lines are drawn through each table, separating the respiration experiments prior to and

[a] For the sake of uniformity, the actual averages for the carbon-dioxide production per half hour are recorded in the tables. It is obvious that in those tests where the averages involve four significant figures, the last figure is not known with great accuracy. On the other hand, when the amount of carbon dioxide is as low as 35 grams per half hour, as occasionally happens, discarding the third figure does not seem justifiable.

subsequent to ration curtailment and subsequent to realimentation. Certain of the animals, namely, Nos. 6, 8, 9, and 12, had two ration curtailments, one on December 22 and one on February 8, and on their tables horizontal lines are drawn to distinguish between the respiration experiments at the two different submaintenance levels.

To indicate the amount of feed received, we have laid upon the several charts blocks representing in rather a general manner the approximate metabolizable energy in the feed per day, blocks necessarily representing average values over periods of several weeks, as outlined in Tables 41 to 44 (see pp. 168 to 171).[a] From these blocks representing the metabolizable energy in feed, the relationship between the energy intake and the various factors of physiological activity, such as pulse-rate, body-weight, and heat-production, may more clearly be noted. Certain special daily feedings, which are of value in considering individual respiration experiments, particularly the feed given a day or two before the respiration experiment, are frequently noted in footnotes in connection with the several tables. The feed was, as a rule, reasonably constant from week to week. (See Tables 3 and 4 for the average water-free substance in feed per day throughout the period of observation.) In the footnotes to the tables the amounts of hay or grain recorded deal with the weight actually eaten per day and not with the weight of water-free substance. Thus, 10 kg. of hay were consumed per day by steer 2 between November 27 and December 22, inclusive, this amount representing the actual weight of hay as eaten and not the water-free substance in the hay. While in the footnotes the actual weight of hay or grain as eaten is recorded, in the feed tables (see pp. 38 and 39) only the water-free substance of feed is considered, irrespective of the character of the feed. Strictly speaking, the water-free substance of hay is very much less digestible than the water-free substance of grain, but it has not seemed advisable to attempt to indicate on the charts anything more than the total metabolizable energy, without discriminating between that furnished by the hay and that furnished by the grain. In general, it may be stated that the feed consisted exclusively of hay through May 12 for steers 1 to 12 and through June 12 for steers A and B. Subsequently all the steers were given varying rations, some with concentrates, steer 10 receiving hay only for a while and others being put on pasture. But, considering that our main interest in the tables and charts is the comparison of the submaintenance period with the maintenance period, it is important to bear in mind that the feed in both of these periods was with all animals exclusively of hay, a fact which simplifies the comparison.

## Consideration of the Normal Standard Metabolism of Steers.

### THE NORMAL STANDARD METABOLISM OF 14 ADULT STEERS ON A MAINTENANCE RATION EXCLUSIVELY OF HAY.

In the course of our investigations we had the opportunity of measuring the standard metabolism of 14 adult steers after a longer or shorter period on a supposedly maintenance ration exclusively of hay. It is of interest, therefore, to compare the measured standard metabolism under such a con-

[a] In these tables are likewise incorporated the values for the water-free substance in feed per day, which have special significance, inasmuch as Professor Armsby's constants for the calorific value of carbon dioxide involve the use of the water-free substance in feed.

dition, for one can consider that exactly the same treatment, so far as the experiments themselves are concerned, was given all the animals, namely, that they had been fed hay for a longer or shorter time and then were placed inside the respiration chamber, allowing for no preliminary training or period of adjustment. Unfortunately, but one day's observation was secured with each of the animals on this basis, although frequently 2, 3, or even 4 half-hour periods (and in one case 5 periods) were secured. These observations were all carried out with steers 1 to 12 between December 3 and December 7, 1918. On January 7, 1920, similar tests of standard metabolism were made with steers A (3 periods) and B (2 periods), each without prior training inside the respiration chamber. Physiologists could not possibly accept such measurements on humans as indices of standard metabolism. The exigencies of experimentation made it necessary for us, certainly with steers 1 to 12, to begin our submaintenance work almost immediately, and we could not carry out more observations upon them. With steers A and B duplicate tests should have been secured. It is only to be said, however, that each day inside the respiration chamber meant a rather serious disturbance in the rationing, which affected the feces excretion, as has already been seen, and hence was to be avoided.

Since in our original plan we purposed carrying 3 animals throughout the entire winter on normal rations, we did not at that time realize the significance of securing more accurate data on all the animals practically simultaneously or within a few days of each other. This point was not sufficiently recognized even with steers A and B. However, it has seemed important to collect the values obtained in these first tests, as they represent for steers 1 to 12 practically the same conditions with regard to previous history of rationing. The first values obtained with steers A and B we believe are not directly comparable with the values for steers 1 to 12, since the hay ration of steers A and B was measurably less effective for maintenance than was that given to the other steers, although we believe that even in the case of steers 1 to 12 the ration was somewhat short of a true maintenance hay ration, if, indeed, such a ration can be secured. Our study, therefore, of the normal metabolism on maintenance rations deals with two sets of values, first, those obtained on all 14 animals prior to any ration curtailment, consisting in every case of observations upon but one experimental day. These observations will give an index of the variability of different animals under exactly the same conditions. Our second, and by far the most important, set of values are those secured in the continued series of observations upon Group I, including the control animals, Nos. 2, 4, and 5, which were carried throughout the first phase of the experimental year (corresponding to the submaintenance periods of Groups II and III) upon a supposedly maintenance ration of hay.

The metabolism measurements secured upon all 14 animals on the first day of their experience inside the respiration chamber have been brought together in Table 61, precisely the same form of table being used which is subsequently used for reporting all of the individual records for the separate steers during the entire season's experimenting. This table records for each steer the live weight, the percentage of empty weight ($W$) to live weight, the body-surface as computed from Moulton's formula, the number of periods of observation, the average carbon-dioxide production per half hour, and the heat-production

computed therefrom, including the total heat-production per 24 hours and that per 500 kg. of body-weight and per square meter of body-surface. In the first place, it is to be noted that the animals had very widely differing body-weights, ranging from 401 kg. with steer 12 to 609 kg. with steer 5. On the other hand, steers A and B were as nearly as possible duplicate animals, their difference in weight being but 30 kg. Practically all of the animals were in a fairly good condition of flesh, as indicated by the percentage of empty weight to live weight, which averaged about 89 per cent in all cases. The body-surface varied essentially with the weight.

TABLE 61.—*Normal, standard metabolism of steers on a maintenance ration exclusively of hay.*

| Steer No. | Date. | Live weight. | Per cent empty weight ($W$) to live weight. | Body-surface ($0.1186W^{\frac{2}{3}}$). | No. of periods. | Average carbon dioxide produced per half hour. | Heat (computed) per 24 hours. | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | Total. | Per 500 kg. | Per sq. meter. |
| | | *kg.* | | *sq. meters.* | | *gm.* | *cal.* | *cal.* | *cal.* |
| 1 | Dec. 7 | 581 | 88 | 5.85 | 1 | 74.5 | 11,100 | 9,600 | 1,900 |
| 2 | Dec. 4 | 470 | 89 | 5.16 | 4 | 74.2 | 11,000 | 11,700 | 2,130 |
| 3 | Dec. 3 | 505 | 89 | 5.39 | 4 | 82.1 | 12,200 | 12,100 | 2,260 |
| 4 | Dec. 4 | 528 | 89 | 5.55 | 2 | 73.0 | 10,800 | 10,200 | 1,950 |
| 5 | Do. | 609 | 89 | 6.07 | 1 | 88.1 | 13,100 | 10,800 | 2,160 |
| 6 | Dec. 7 | 435 | 88 | 4.88 | 3 | 66.3 | 9,900 | 11,400 | 2,030 |
| 7 | Dec. 6 | 467 | 89 | 5.14 | 5 | 69.5 | 10,300 | 11,000 | 2,000 |
| 8 | Do. | 466 | 89 | 5.13 | 3 | 78.1 | 11,600 | 12,400 | 2,260 |
| 9 | Do. | 574 | 87 | 5.76 | 4 | 85.0 | 12,600 | 11,000 | 2,190 |
| 10 | Dec. 5 | 594 | 89 | 5.97 | 3 | 97.7 | 14,500 | 12,200 | 2,430 |
| 11 | Do. | 520 | 89 | 5.50 | 3 | 73.6 | 11,000 | 10,600 | 2,000 |
| 12 | Do. | 401 | 87 | 4.61 | 4 | 61.9 | 9,200 | 11,500 | 2,000 |
| | Average | 513 | 89 | 5.42 | 3 | 77.0 | 11,400 | 11,200 | 2,110 |
| A[1] | Jan. 7 | 591 | 89 | 5.95 | 3 | 84.5 | 12,600 | 10,700 | 2,120 |
| B[1] | Do. | 561 | 89 | 5.76 | 2 | 96.6 | 14,400 | 12,800 | 2,500 |
| | Average | 576 | 89 | 5.86 | 3 | 90.6 | 13,500 | 11,800 | 2,310 |
| | Grand average | 522 | 89 | 5.48 | 3 | 78.9 | 11,700 | 11,300 | 2,140 |

[1] The pulse-rate of both steers A and B was 49 beats per minute. Pulse-records were not secured for steers 1 to 12 on the dates given above.

Special attention must be given to the carbon-dioxide measurement and to the heat-production computed therefrom. Under the head of the average carbon dioxide produced per half hour we find wide ranges in values, extending from 61.9 grams with steer 12, as a matter of fact, the smallest animal, to 97.7 grams with steer 10, which is one of the largest animals, weighing within 15 kg. of the heaviest steer. It is obvious, therefore, that the carbon-dioxide production *per se*, as directly measured, is not a basis for comparison, because no correction for the size of the animal is introduced in this measurement. As we are but indirectly interested in the carbon-dioxide production, however, we may pass directly to the computed heat-production, which varies with these animals directly as the carbon-dioxide production, since the calorific value of carbon dioxide, namely, 3.1 calories per gram of carbon dioxide, is taken as constant for all the animals. The heat-production per 24 hours ranges from 9,200 calories to 14,500 calories, the average being 11,400 calories for the first 12 animals (with an average weight of 513 kg.)

and 13,500 calories for steers A and B, a slightly higher average which may obviously be in large part ascribed to the somewhat higher average body-weight, i. e., 576 kg. A better method of comparison is obtained when the heat-production is computed per 500 kg. of body-weight, in the attempt to equalize inequalities in body-weight. On this basis wide variations, such as were noted in the total heat-production, are not found, the values per 500 kg. of body-weight per 24 hours for steers 1 to 12 ranging only from 9,600 calories with steer 1 to 12,400 calories with steer 8, the average being 11,200 calories. The values for steers A and B, 10,700 calories and 12,800 calories, respectively, do not differ so widely, and for these 2 steers the average is 11,800 calories, a value essentially that found on the average for the first 12 steers. At first sight, therefore, this method of computation would indicate a close agreement between the two groups, even if the second group was relatively small. On the other hand, the extremely low value of 9,600 calories with steer 1 and the maximum value of 12,800 calories with steer B must not be overlooked. When we pass to the supposedly much better method of comparison, namely, on the basis of body-surface area, we find that the variability is not measurably less. Thus, in the first group of 12 steers the lowest value is 1,900 calories per square meter per 24 hours with steer 1 and the highest value is 2,430 calories with steer 10, the values showing a distinct tendency to group around 2,100 calories. The average for the first group of 12 animals is 2,110 calories, while the average for steers A and B is 2,310 calories, with rather a wide difference between these two animals.

Without at this time going further into the relative merits of comparing animals on the basis of per unit of body-weight or body-surface, it can be seen that the average heat-production per 500 kg. of body-weight per 24 hours is 11,200 calories for steers 1 to 12, and 11,800 calories for steers A and B, giving as a grand average for all 14 animals 11,300 calories. Similarly, on the surface-area basis, the grand average is 2,140 calories. These two general values of 11,300 calories and 2,140 calories may be taken as representing the average standard metabolism of animals measured under the conditions we employed in this research, namely, the standard metabolism measured during the animal's first experience inside the respiration chamber, following a rather prolonged feeding upon hay only in an amount probably somewhat less than maintenance in the case of steers 1 to 12 and in the case of steers A and B without doubt measurably less than maintenance.

The individual variations from these two average values, which are rather considerable, may be due to several causes; in the first place, inequality in activity or restlessness. The degree of activity admittedly plays a very large rôle in experiments when animals are placed for the first time inside a respiration chamber. Consequently, we may not consider that this series of observations is ideal in affording a measure of the standard metabolism. Secondly, the variations may represent true individual differences. This last conception is strongly opposed by many physiologists, who believe that by computing the heat-production either per unit of mass or per unit of surface-area, particularly per unit of surface-area, all individuals are equalized, and that this method of computation gives a constant which is applicable to all individuals. With this conception we are not at all in sympathy. Experiments at the Nutrition Laboratory with humans have shown that this is far

from the case. A careful biometric analysis of the Nutrition Laboratory data[a] has proved without doubt that the metabolism with humans depends upon at least four separate factors—age, weight, height, and sex. There is no reason for thinking that similar factors may not play a rôle in animal nutrition. While it is true that the computation of the metabolism per 500 kg. of body-weight or per square meter of body-surface does approximately equalize the differences in individuals, the variability here shown may be taken of itself as an index that a constant is not by any means obtained, and we must recognize instantly the strong probabilities of differences in individuality in the standard metabolism. Every possible method of comparison must be used, however, in analyzing our data secured in the long series of observations made on our different animals upon different nutritive planes, and we therefore desire to compare the individuals not only with regard to their own too rapidly and too hastily determined standard metabolism prior to the ration curtailment, but likewise we desire particularly to compare the animals subjected to submaintenance rations with the group of control steers which were carried along with them throughout the entire winter. It is with these ultimate comparisons in mind, therefore, that we have presented a consideration of the standard metabolism as measured in the first part of the experimental season, when the animals had their first experience in the respiration chamber.

### COURSE OF STANDARD METABOLISM OF THREE ADULT STEERS DURING FIVE MONTHS ON A MAINTENANCE RATION EXCLUSIVELY OF HAY, FOLLOWED BY THREE AND ONE-HALF MONTHS ON FATTENING RATIONS, GROUP I.

Normal data with regard to the gaseous metabolism and energy transformations of steers under the special conditions of our experiments were lacking, and we did not feel justified in relying solely upon the individual standard metabolism measurements made with each of our 14 steers on the first day of their experience inside the respiration chamber, because of the possibilities of errors in such a single set of determinations caused by the novelty of the experience and possibly by differences in the previous ration, although the determinations were made upon rather a large number of animals which had in all cases been fed hay exclusively. Furthermore, since submaintenance was to be continued for a period of months involving considerable climatic changes, a control set seemed especially desirable. From previous experience with humans it was expected that the reduction in ration would have a rather pronounced influence upon the metabolism, especially since our project involved a considerable loss in weight on the part of the animals subjected to the reduced ration. Consequently, it became necessary to compare these animals in their physiological states of full maintenance and submaintenance, but it was deemed of even greater importance to study also a group of control animals to which all changes in the several groups on restricted rations could be directly referred. The normal data reported in Table 61 were, therefore, supplemented by continuous observations on a group of control steers, Nos. 2, 4, and 5, which received for several months a ration exclusively of hay. A knowledge of the normal standard metabolism of this group was especially

[a] Harris and Benedict, Carnegie Inst. Wash. Pub. No. 279, 1919.

important, since the feeding with all animals for the greater part of the year was to be confined exclusively to mixed hay. The number of gaseous-metabolism experiments made by other investigators with hay alone is relatively small, and at the beginning of our study it did not seem justifiable to use average values derived from the earlier literature on the subject as a basis of reference for our animals. Furthermore, little was known with regard to the influence of environmental temperature, which must of necessity vary during a New England winter, and the possibility of a seasonal variation in metabolism could not be ruled out, facts which also made the study of the group of normal control animals essential.

For a period of approximately 5 months the control animals in Group I were supposedly on a maintenance ration of hay alone, after which time two of them were given heavy grain rations for fattening and one was put on pasture. In computing the rations for the maintenance period, we used well-known modern standards for energy requirements, considering constancy in body-weight as an index of maintenance. When changes occurred in the body-weight from time to time, it was necessary to alter the amounts of feed given. We believe that these alterations in rations may have been made too suddenly, and furthermore, that the hay did not furnish sufficient protein, for although in general there was a reasonable constancy in the weight, there must have been a very considerable loss in body-protein, a fact clearly brought out in the second series of experiments with steers A and B, with which it was found that a ration of hay alone did not prevent nitrogen-loss. Armsby's experience[a] is quite in line with this, since he found that although the first digestion experiments were made with hay exclusively, it was necessary subsequently to add a small amount of linseed meal to keep up the nitrogen balance. We did not make this addition of meal to our rations. This omission is a defect in our experiments, but we believe that our system of controls was such that this defect does not seriously vitiate our general deductions.

From the body-weight, which, as is common, was used as an index of maintenance, and from the average computed digestibility of the ration, one can estimate by standard formulæ the probable 24-hour needs of an animal. A direct measurement of the animal's needs with a respiration apparatus is, however, infinitely preferable, and since all of our submaintenance animals were to be studied directly, it seemed necessary to study similarly a group of normal animals. The three steers in Group I were studied as regularly and as frequently as were the submaintenance animals in Groups II and III.

The desirability of presenting the data both in tables and in charts has already been discussed. The data collected for the control steers are given in tabular form in Tables 62, 63, and 64, and are plotted graphically in Figures 25, 26, and 27.

### The Course of the Standard Metabolism of Steer 2.

Considering, first, the experimental series with steer 2 (as reported in Table 62 and Fig. 25), we observe that although the ration was supposed to be a maintenance ration, the animal actually lost in weight, so that the first weight is a maximum, exceeded only by the last weight of the series, July 17. Between January 8 and May 10 the animal remained reasonably

[a] Armsby and Fries, U. S. Dept. Agric., Bureau Animal Industry, Bull. 51, 1903, p. 9.

constant in weight, especially when it is considered that the weights recorded in these tables represent the actual weights found on the mornings of the respi-

TABLE 62.—*Body-weight, body-surface, pulse-rate, and standard heat-production per 24 hours, steer 2.*

| Date. | Live weight. | Per cent empty weight ($W$) to live weight. | Body-surface ($0.1186\ W^{2/3}$) | No. of periods. | Average temperature of chamber. | Average carbon-dioxide produced per half-hour. | Heat (computed)[1] per 24 hours. | | | Average pulse-rate per minute. |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | Total. | Per 500 kg. | Per sq. meter. | |
| 1918–19. | *kg.* | | *sq. m.* | | °*C.* | *gm.* | *cal.* | *cal.* | *cal.* | |
| Dec. 4[3] | [2]470 | 89 | 5.16 | 4 | 12.0 | 74.2 | 11,000 | 11,700 | 2,130 | ..... |
| Jan. 8[4] | 443 | 89 | 4.97 | 2 | ..... | 86.7 | 12,900 | 14,600 | 2,600 | 41 |
| Jan. 20 | 444 | 89 | 4.98 | 1 | 17.3 | 70.3 | 10,500 | 11,800 | 2,110 | 39 |
| Jan. 30 | 440 | 89 | 4.95 | 4 | 15.5 | 66.7 | 9,900 | 11,300 | 2,000 | 41 |
| Feb. 12 | 441 | 89 | 4.95 | 3 | 6.4 | 50.8 | 7,600 | 8,600 | 1,540 | 43 |
| Feb. 19 | 439 | 89 | 4.94 | 4 | 10.7 | 48.9 | 7,300 | 8,300 | 1,480 | 41 |
| Feb. 26 | 434 | 89 | 4.91 | 3 | 14.5 | 62.7 | 9,300 | 10,700 | 1,890 | 40 |
| Mar. 6 | 442 | 89 | 4.96 | 3 | 12.6 | 64.0 | 9,500 | 10,700 | 1,920 | 40 |
| Mar. 14 | 436 | 89 | 4.92 | 5 | 10.8 | 62.0 | 9,200 | 10,600 | 1,870 | 40 |
| Apr. 5 | 423 | 89 | 4.83 | 3 | 16.4 | 65.6 | 9,800 | 11,600 | 2,030 | 44 |
| Apr. 7 | 441 | 89 | 4.95 | 3 | 14.3 | 69.6 | 10,400 | 11,800 | 2,100 | 42 |
| Apr. 14 | 445 | 89 | 4.99 | 3 | 18.2 | 55.7 | 8,300 | 9,300 | 1,660 | 43 |
| Apr. 17 | 439 | 89 | 4.94 | 3 | 14.7 | 63.9 | 9,500 | 10,800 | 1,920 | 43 |
| Apr. 30 | 445 | 89 | 4.99 | 3 | 17.8 | 61.7 | 9,200 | 10,300 | 1,840 | 45 |
| May 10[5] | 451 | 89 | 5.02 | 3 | 17.8 | 67.8 | 10,100 | 11,200 | 2,010 | 46 |
| July 17[6] | 488 | 89 | 5.28 | 3 | 28.1 | 76.2 | 11,300 | 11,600 | 2,140 | 72 |
| Av., Jan. 20 to May 10 | ..... | ..... | ..... | ..... | ..... | 62.3 | 9,300 | 10,500 | 1,870 | ..... |

[1] Assumed 3.1 calories per gram $CO_2$ for all dates.
[2] Steer had about 10 kg. hay per day, Nov. 27 to Dec. 2, inclusive; on Dec. 3 had 4.0 kg. hay.
[3] Weight on Dec. 2; not weighed Dec. 4.
[4] Steer had about 8 kg. hay per day, Dec. 28 to May 7, inclusive; had 9.4 kg. hay, May 8, and 5.0 kg., May 9.
[5] Steer had been on pasture since May 20.

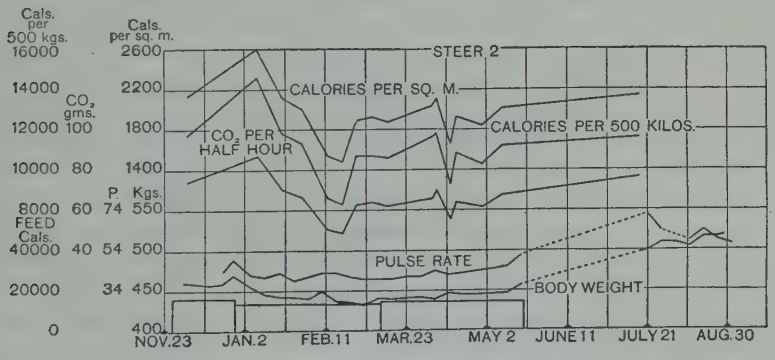


FIG. 25.—Curves for body-weight, pulse-rate per minute, carbon-dioxide production per half hour, and heat-production per 500 kg. of body-weight per 24 hours and per square meter of body-surface per 24 hours, and blocks for metabolizable energy in feed per day, steer 2.

Steer 2 was turned out to pasture on May 20 and data for the metabolizable energy in feed after this date are not available.

ration experiments and are not averages for several days. Based, then, primarily upon the body-weight, it can be seen that the ration was a maintenance ration after January 8. After May 19 steer 2 went to pasture and the only

respiration experiment we have with this animal during the realimentation period was on July 17, at which time he had increased about 30 to 40 kg. in weight.

In spite of the use of electrical heaters to control the temperature of the chamber, the range in temperature was considerable, since on February 12 the apparatus could not be warmed above 6.4° C., while on July 17, owing to the excessive heat outside, the experiment had to be made at a chamber temperature of 28.1° C.

The average carbon-dioxide production per half hour extends through rather a wide range. A minimum of 48.9 grams is noted on February 19 and maximum values are recorded on January 8 and July 17, the latter during the period on pasture. In a certain sense, then, one might consider that the range found here represents that which would normally be noted with a steer not undergoing any ration restrictions. The low value of 48.9 grams, which was the average of 4 periods on February 19, is well substantiated by a value of 50.8 grams, the average of 3 periods on February 12. On the other hand, the high value of 86.7 grams on January 8, which is the average of but 2 periods, might be questioned. As we have no reason to note from the protocols any justification for excluding this particular experiment, however, it must be included and considered as an indication of the possible variation normally to be expected. The value of 74.2 grams on December 4 is coincidental with the highest body-weight except for that recorded on the last day, and since we believe that our maintenance rations were not true maintenance, in that there was undoubtedly a loss of nitrogen and possibly of body-fat, it is reasonable to presume that steer 2 was on a slightly higher nutritive plane on December 4 than subsequently until July 17. In the July experiment the animal had been at pasture for 2 months, and although he had not gained excessively in weight and had hardly more than reached his original weight, nevertheless the high value of 76.2 grams is in line with the increased weight, as is also the heat-production computed from the carbon dioxide. In passing, attention should be called also to the extraordinarily high value for the pulse-rate on July 17, although special discussion of the pulse-rate has already been given. Excluding the first two values and the last value, the average carbon-dioxide production for the rest of the year is reasonably constant at about 62 grams.

Special attention, however, must be given to the very low values of February 12 and 19. In connection with the possible influence of environmental temperature upon the metabolism of the animal, it is important to note here that on these two days two of the lowest temperatures recorded appear, but, as pointed out in an earlier section, these and other similar data make it impossible for us to draw any definite deductions as to the influence of environmental temperature, for the picture is by no means clear, especially as it is diame - rically opposite to all accepted doctrines of heat-production as related to environmental temperature.

While the average carbon-dioxide production per half hour furnishes a good index for comparison of the animal in different periods, for a more general comparison it is important to note the total heat-production per 24 hours, as well as that per 500 kg. of body-weight and per square meter of body-surface per 24 hours, the last two instances representing a supposedly greater refine-

ment in computing the heat, in an attempt to equalize the animals, if possible, and make them even more comparable. In computing the heat from the carbon-dioxide production it has been assumed throughout the entire series of observations that each gram of carbon dioxide is accompanied by the evolution of 3.1 calories, with an animal in the state of nutrition and under the conditions of feeding obtaining with steer 2. At no time did he receive grain. He was on a supposedly maintenance ration of hay alone during the entire series of respiration experiments, with the single exception of that on July 17, which followed several weeks on pasture. Although one might contend that when the steer was on pasture a somewhat different calorific value for carbon dioxide might be justifiable, in the light of the earlier discussion (see p. 206) we have felt that it was unwise to make any arbitrary selection of a factor. The heat-production is computed directly, therefore, from the carbon-dioxide production per half hour, multiplying it by 48 to bring it to the 24-hour basis, and then converting it to heat by multiplying by the factor 3.1. From the method of computation it is obvious that the heat values are directly proportional to the average values for the carbon-dioxide production per half hour. Consequently the high heat-values are coincidental with the high values observed for carbon dioxide, and the whole discussional treatment of separate days applies to the total heat-production exactly as it did to the carbon-dioxide production.

For purposes of subsequent comparison, the computations on the basis of per 500 kg. of body-weight and per square meter of body-surface are of unusual interest. Steer 2 weighed somewhat under 500 kg., and consequently the heat-production per 500 kg. is somewhat greater than the total heat-production in every case. It is important to note here that in this computation we have not, as Professor Armsby strongly recommends, used the two-thirds power of the body-weight, for we believe that if emphasis is to be laid upon the heat-production per square meter of body-surface, it is much better to make this comparison with the more refined methods, employing the formula of Moulton, rather than to use the cruder method of the two-thirds power of the body-weight. We have, therefore, made the computations per 500 kg. directly, a method which involves *only* body-weight, and any computations involving the use of surface-area we have carried out by the better methods suggested by Moulton, using the computed surface-area. Under these circumstances it is obvious that the relative heat-values on the basis of per 500 kg. of body-weight are proportionately identical with the total heat-values, and in turn proportionately identical with the values for the carbon-dioxide production per half hour. It can be seen that steer 2 had a standard metabolism for the greater part of the year of not far from 10,000 calories per 500 kg. of body-weight. This value it will be important to compare with the values secured with the two other animals, Nos. 4 and 5, on normal maintenance rations, thus contributing to the establishment of normal standards of reference for the submaintenance animals.

Finally, using the body-surface as computed by Moulton's formula, the computation of the heat per square meter of body-surface has been made in the next to the last column of Table 62. Here, although the five-eighths power of the body-weight enters into the computation and the body-surface varies somewhat, we can see that in general the large values for the heat-pro-

duction per square meter of body-surface are coincidental with the high values for the average carbon-dioxide production per half hour, and little is to be gained by comparison between themselves of the figures for the heat-production per square meter. The average values are, however, of importance for comparison with other animals, and it can be seen that in general steer 2 had a standard metabolism of 1,870 calories per square meter of body-surface per 24 hours.

For purposes of subsequent comparison, then, an average has been obtained by an admittedly debatable procedure, namely, by excluding the first two values for December 4 and January 8 and that for July 17. As recorded in the last line of Table 62, therefore, steer 2 had an average normal standard heat-production for the greater part of the winter of 10,500 calories per 500 kg. of body-weight and 1,870 calories per square meter of body-surface per 24 hours.

### The Course of the Standard Metabolism of Steer 4.

The data for the normal control steer, No. 4, are incorporated in Table 63 and charted in Fig. 26. Here the situation is much the same as it was with steer 2. Although the ration was supposed to have been a maintenance ration, there was a fall in weight after the first week, as will be seen by reference to the body-weight curve for steer 4 in Figs. 19 and 26 (see pp. 88 and 240). The temperature in the apparatus underwent an unavoidably wide range, as in the case of steer 2, with a minimum of 8.4° C. on February 28 and a maximum of 29.6° C. on June 4. A direct comparison of the metabolism during these temperature extremes is not possible, however, since in the latter period during the high temperatures the animal was receiving a heavy grain ration.

The average carbon-dioxide production per half hour remains reasonably uniform up to the period of grain feeding, i. e., until May 15. Two very low values appear, however, on February 17 and February 28, with the lowest value of all, 44.5 grams, on March 12. Unlike the case of steer 2, there are no supporting data to confirm the very low figure for this day, which is, however, the average of three periods. Again we have no alternative except to present the data and to assume that they indicate the possible extreme variation in metabolism normally to be expected in standard metabolism experiments. Considering the values up to and including May 8, we find that the metabolism is reasonably uniform, with perhaps a slight tendency for the carbon-dioxide production to be somewhat lower during the months of February, March, and April. With the feeding of grain striking increases in the carbon-dioxide production occur, although again the value of 71.8 grams on June 4 is difficult to explain, coming as it does between the higher values of 84.9 grams on May 27 and 89.7 grams on June 11. Very high values of 90 grams or over appear in the last three experiments.

The computation of the heat-production from the carbon-dioxide production of this animal is on a slightly different basis than with steer 2, inasmuch as, based upon Professor Armsby's results, we feel that during the grain-feeding period the calorific value of carbon dioxide is nearer 2.9 calories per gram than 3.1 calories. Hence from May 15 on all calculations are based upon the lower factor. Since this animal weighed essentially 500 kg. during the main-

tenance period, there is little difference between the total heat-production per 24 hours and that per 500 kg. of body-weight. On the average the heat-production per 500 kg. of body-weight per 24 hours is 9,700 calories, but there is an extraordinarily low value of 6,700 calories per 500 kg. on March 12, referable obviously to the very low carbon-dioxide production per half hour of 44.5

TABLE 63.—*Body-weight, body-surface, pulse-rate, and standard heat-production per 24 hours, steer 4.*

| Date. | Live weight. | Per cent empty weight ($W$) to live weight. | Body-surface ($0.1186 W^{\frac{2}{3}}$). | No. of periods. | Average temperature of chamber. | Average carbon dioxide produced per half hour. | Heat (computed) per 24 hours.[1] | | | Av. pulse-rate per minute. |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | Total. | Per 500 kg. | Per sq. meter. | |
| 1918–19. | *kg.* | | *sq. m.* | | *°C.* | *gm.* | *cal.* | *cal.* | *cal.* | |
| Dec. 4[2] | [3]528 | 89 | 5.55 | 2 | ..... | 73.0 | 10,800 | 10,200 | 1,950 | ..... |
| Jan. 8[4] | 508 | 89 | 5.41 | 1 | ..... | 77.8 | 11,600 | 11,400 | 2,140 | 40 |
| Jan. 17 | 498 | 89 | 5.35 | 5 | 13.7 | 76.9 | 11,400 | 11,400 | 2,130 | 38 |
| Jan. 25 | 501 | 89 | 5.37 | 3 | 12.2 | 73.5 | 10,900 | 10,900 | 2,030 | 39 |
| Feb. 3 | 510 | 89 | 5.43 | 3 | 14.3 | 73.4 | 10,900 | 10,700 | 2,010 | 41 |
| Feb. 7 | 495 | 89 | 5.33 | 4 | 10.0 | 67.6 | 10,100 | 10,200 | 1,890 | 41 |
| Feb. 17 | 500 | 89 | 5.36 | 4 | 13.5 | 53.8 | 8,000 | 8,000 | 1,490 | 40 |
| Feb. 28 | 491 | 89 | 5.30 | 3 | 8.4 | 55.5 | 8,300 | 8,500 | 1,570 | 41 |
| Mar. 8 | 495 | 89 | 5.33 | 3 | 15.3 | 61.3 | 9,100 | 9,200 | 1,710 | 43 |
| Mar. 12 | 490 | 89 | 5.29 | 3 | 13.4 | 44.5 | 6,600 | 6,700 | 1,250 | 44 |
| Apr. 7 | 492 | 89 | 5.31 | 3 | 16.2 | 63.1 | 9,400 | 9,600 | 1,770 | 47 |
| Apr. 10 | 489 | 89 | 5.29 | 3 | 15.0 | 64.2 | 9,600 | 9,800 | 1,810 | 47 |
| Apr. 21 | 494 | 89 | 5.32 | 3 | 18.3 | 63.4 | 9,400 | 9,500 | 1,770 | 46 |
| May 1 | 493 | 89 | 5.32 | 3 | 15.4 | 70.1 | 10,400 | 10,500 | 1,950 | 45 |
| May 8[4] | 490 | 89 | 5.29 | 3 | 18.3 | 61.7 | 9,200 | 9,400 | 1,740 | ..... |
| Av., Jan. 8 to May 8 | ..... | ..... | ..... | ..... | ..... | 64.8 | 9,600 | 9,700 | 1,800 | ..... |
| May 15[5] | 500 | 89 | 5.36 | 3 | 17.8 | 71.6 | 10,000 | 10,000 | 1,870 | 57 |
| May 27[7] | 491 | 89 | 5.30 | 3 | 23.1 | 84.9 | 11,800 | 12,000 | 2,230 | ..... |
| June 4 | 497 | 89 | 5.34 | 3 | 29.6 | 71.8 | 10,000 | 10,100 | 1,870 | 73 |
| June 11 | 508 | 89 | 5.41 | 3 | 23.9 | 89.7 | 12,500 | 12,300 | 2,310 | ..... |
| June 20 | 525 | 89 | 5.53 | 3 | 27.6 | 79.3 | 11,000 | 10,500 | 1,990 | 71 |
| June 25 | 546 | 90 | 5.70 | 3 | 28.9 | 91.3 | 12,700 | 11,600 | 2,230 | 78 |
| July 1[8] | 551 | 90 | 5.74 | 3 | 24.4 | 104.3 | 14,500 | 13,200 | 2,530 | 75 |
| July 12 | 558 | 90 | 5.78 | 3 | 21.8 | 93.3 | 13,000 | 11,600 | 2,250 | 78 |
| Av., May 15 to July 12 | ..... | ..... | ..... | ..... | ..... | 85.8 | 11,900 | 11,400 | 2,160 | ..... |

[1] In Tables 63 to 80, heat computed by assuming 3.1 calories per gram $CO_2$ for all dates through May 12, and 2.9 calories for all dates after May 12, unless stated otherwise.

[2] Steer had from 10 to 12 kg. hay per day, Nov. 27 to Dec. 2, inclusive; 4.9 kg. hay, Dec. 3.

[3] Weight on Dec. 2; not weighed on Dec. 4.

[4] Steer had 8 to 9 kg. hay per day, Dec. 28 to May 5, inclusive, except when evening feed was withheld prior to a respiration experiment, when this amount was made up on day following experiment.

[5] Steer had 8.4 kg. hay, May 6, and 4.2 kg., May 7.

[6] Steer had 12.4 kg. hay, May 9; 9.9 kg. hay, May 10; 9.3 kg. hay, May 11; 10.4 kg. hay, May 12; 4.7 kg. hay and 1.0 kg. grain, May 13; on May 14 had 2.0 kg. grain but no hay, as some hay was left over from evening before.

[7] Steer had 7.1 kg. hay and 5.0 kg. grain, May 25; 3.5 kg. hay and 2.5 kg. grain, May 26.

[8] Steer had about 8 kg. hay and 9 to 10 kg. grain, June 26 to 29, inclusive; on June 30 had 2.9 kg. hay and 5.0 kg. grain.

grams, noted above. After May 12, when the grain rations were given, there is a noticeable increase not only in the total heat-production, but likewise in the heat-production per 500 kg. of body-weight. Obviously, as the animal increases in weight from about 500 kg. to 558 kg. on the last day, we would expect a larger amount of heat to be produced. The total heat-production does increase, since the last three figures are practically 13,000 calo-

ries or over. The increase in weight is about 10 per cent. The increase in the total heat-production is not far from 25 per cent. On the basis of the heat-production per 500 kg. of body-weight, since the animal weighed not far from that on the average, practically the same proportion holds true, the increase amounting to 18 per cent. On the basis of weight only, therefore, the heat-production is perceptibly higher during the grain period.

When we consider the heat-production per square meter of body-surface per 24 hours, we see that there are a series of values from February 17 to March 12, inclusive, that are very low, averaging 1,500 calories. This is in rather striking contrast to the average of 2,040 calories for the first five experiments (excluding December 4) and the average of 1,810 calories for the last five experiments prior to fattening. These low values would more or less suggest a seasonal variation in metabolism, with a low heat-production both per 500 kg. of body-weight and per square meter of body-surface during the

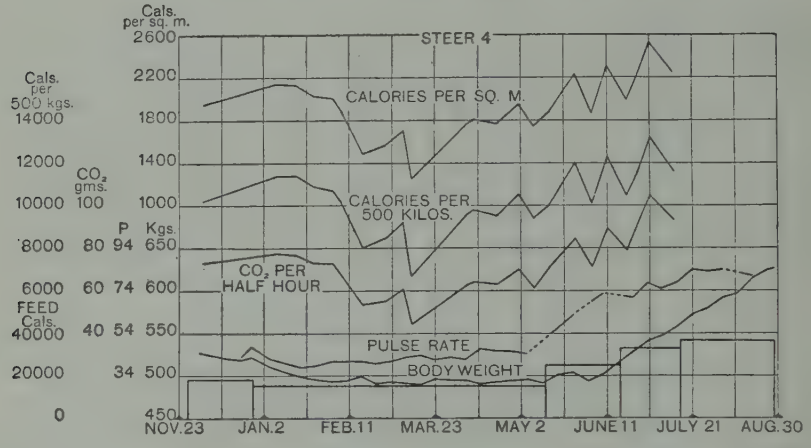


FIG. 26.—Curves for body-weight, pulse-rate per minute, carbon-dioxide production per half hour, and heat-production per 500 kg. of body-weight per 24 hours and per square meter of body-surface per 24 hours, and blocks for metabolizable energy in feed per day, steer 4.

latter part of February and the first part of March. It is an extraordinary fact, however, that actually the lowest temperature of the apparatus is coincidental with the low heat-production during this time, contrary to all accepted views with regard to the relationship between environmental temperature and metabolism. The possibilities of experimental error seem practically ruled out, since the apparatus was frequently checked by carbon-dioxide control tests, which almost invariably gave satisfactory results. Indeed, a series of experiments was not run unless the check tests were satisfactory. We believe that the interspersing of control tests in any series of experiments is absolutely essential with any type of apparatus. The expense involved is very great, but the insurance of a perfectly functioning apparatus more than amply repays for the time and labor put upon such control tests. The heat-production per square meter of body-surface per 24 hours during the supermaintenance feeding-period after May 15 is noticeably greater than at any other time,

rising toward the end to an average of not far from 2,300 to 2,400 calories, thus proving that there is a distinctly higher metabolic plane during the supermaintenance period.

At this point it is necessary to consider the errors possible in measuring the metabolism during the realimentation period. Is the carbon-dioxide production a true index of metabolic activity at this time? During the period of supermaintenance feeding with grain rations there is an extensive fermentation of carbohydrate, accompanied by the liberation of a large amount of carbon dioxide not resulting from processes of oxidation. To what extent this fermentation and liberation of carbon dioxide holds after feed has been withheld for 24 hours is not exactly determined. We believe, however, from the evidence put forward elsewhere in this report (see p. 215), and particularly from the evidence in the experiments of Professor Armsby, that this process can not play a very heavy rôle, and that by making due allowance for the change in the calorific value of carbon dioxide, i. e., by lowering it from 3.1 calories per gram to 2.9 calories, we have in all probability completely compensated for any increase in carbon-dioxide production due to fermentation. It is desirable at this point, however, to anticipate our later discussion and state that we believe we are dealing in the grain-feeding period with a distinctly higher metabolic plane, with more active metabolic processes, as indicated by the increased carbon-dioxide production, fully substantiated by the pronounced increase in pulse-rate shown by these steers. The correlation between pulse-rate and metabolism has been the subject of a great deal of discussion and experimental treatment with humans, and this correlation is found to be very high. Without pulse-records the carbon-dioxide figures alone would have very much less value.

### The Course of the Standard Metabolism of Steer 5.

The data for the third normal control animal, steer 5, are given in Table 64, and have been graphically represented in Fig. 27. The temperature of the apparatus ranges from 7.5° C. to 29.4° C. The course of the body-weight changes and their bearing upon the fact that the ration was probably not quite a maintenance ration have already been discussed. This steer was the heaviest of the control animals, weighing about 600 kg., and although we question whether the ration was a true maintenance ration, we find that the general condition of the animal remains essentially constant until the fattening period begins. We are dealing here with a larger animal than steers 2 and 4, and hence larger amounts of carbon dioxide are produced on the average. With steer 5 the carbon-dioxide production per half hour up to and including May 7 ranges from a minimum of 53.8 grams on February 27 to a maximum of 88.1 grams on December 4. It is again to be observed that with all three control animals relatively high values are found on the first day of experimenting. This is probably due in part to the fact that the animals were upon a slightly higher nutritive plane, but it is probably also in part due to the fact that they might not have been so thoroughly accustomed to the apparatus as they were later. Excluding the value for December 4, which is probably a little too high, the range in the carbon-dioxide production of steer 5 from January 13 on is not pronouncedly different from that of the two

other animals. Singularly enough, two low values are found on February 21 and February 27, just as were found with steers 2 and 4 about this time, and these low values are again coincidental with fairly low chamber temperatures.

During the maintenance period the total heat-production per 24 hours averages 10,600 calories (not including the value for December 4), a value larger than that found with either of the smaller animals, No. 2 or 4. On the

TABLE 64.—*Body-weight, body-surface, pulse-rate, and standard heat-production per 24 hours, steer 5.*

| Date. | Live weight. | Per cent empty weight ($W$) to live weight. | Body-surface ($0.1186\ W^{\frac{2}{3}}$). | No. of periods. | Average temperature of chamber. | Average carbon dioxide produced per half hour. | Heat (computed) per 24 hours. | | | Average pulse-rate per minute. |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | Total. | Per 500 kg. | Per sq. meter. | |
| 1918–19. | *kg.* | | *sq. m.* | | *°C.* | *gm.* | *cal.* | *cal.* | *cal.* | |
| Dec. 4[1] | [2]609 | 89 | 6.07 | 1 | ..... | 88.1 | 13,100 | 10,800 | 2,160 | ..... |
| Jan. 13[3] | 590 | 89 | 5.95 | 1 | 7.5 | 82.6 | 12,300 | 10,400 | 2,070 | 39 |
| Jan. 21 | 567 | 89 | 5.80 | 2 | 13.0 | 78.0 | 11,600 | 10,200 | 2,000 | 37 |
| Jan. 27 | 575 | 89 | 5.85 | 2 | 12.0 | 78.0 | 11,600 | 10,100 | 1,980 | 40 |
| Feb. 8 | 592 | 89 | 5.96 | 4 | 10.5 | 64.4 | 9,600 | 8,100 | 1,610 | 40 |
| Feb. 14 | 592 | 89 | 5.96 | 3 | 12.9 | 70.7 | 10,500 | 8,900 | 1,760 | 39 |
| Feb. 21 | 592 | 89 | 5.96 | 3 | 13.7 | 56.7 | 8,400 | 7,100 | 1,410 | 38 |
| Feb. 27 | 572 | 89 | 5.83 | 3 | 10.9 | 53.8 | 8,000 | 7,000 | 1,370 | 39 |
| Mar. 7 | 596 | 89 | 5.98 | 3 | 13.1 | 73.6 | 11,000 | 9,200 | 1,840 | 38 |
| Mar. 13 | 591 | 89 | 5.95 | 3 | 14.1 | 68.4 | 10,200 | 8,600 | 1,710 | 40 |
| Apr. 5 | 576 | 89 | 5.86 | 3 | 15.8 | 78.9 | 11,700 | 10,200 | 2,000 | 39 |
| Apr. 8 | 582 | 89 | 5.90 | 3 | 17.4 | 78.2 | 11,600 | 10,000 | 1,970 | 41 |
| Apr. 21 | 585 | 89 | 5.92 | 3 | 18.6 | 74.1 | 11,000 | 9,400 | 1,860 | 43 |
| May 1 | 585 | 89 | 5.92 | 2 | 18.0 | 77.8 | 11,600 | 9,900 | 1,960 | 43 |
| May 7[4] | 590 | 89 | 5.95 | 3 | 17.9 | 62.4 | 9,300 | 7,900 | 1,560 | 47 |
| Av., Jan. 13 to May 7 | ..... | ..... | ..... | ..... | ..... | 71.3 | 10,600 | 9,100 | 1,800 | ..... |
| May 15[5] | 590 | 89 | 5.95 | 3 | 19.6 | 84.9 | 11,800 | 10,000 | 1,980 | ..... |
| May 27 | 580 | 89 | 5.88 | 3 | 25.0 | 81.3 | 11,300 | 9,700 | 1,920 | 56 |
| June 5 | 587 | 89 | 5.92 | 3 | 29.4 | 87.5 | 12,200 | 10,400 | 2,060 | 64 |
| June 11 | 590 | 89 | 5.95 | 3 | 21.3 | 95.8 | 13,300 | 11,300 | 2,240 | 70 |
| June 20 | 615 | 89 | 6.10 | 3 | 27.7 | 92.9 | 12,900 | 10,500 | 2,110 | 61 |
| June 25 | 630 | 89 | 6.20 | 3 | 26.5 | 106.0 | 14,800 | 11,700 | 2,390 | 70 |
| July 7 | 649 | 90 | 6.35 | 3 | 27.1 | 104.4 | 14,500 | 11,200 | 2,280 | 68 |
| July 12 | 648 | 90 | 6.35 | 3 | 25.2 | 106.6 | 14,800 | 11,400 | 2,330 | 68 |
| Av., May 15 to July 12 | ..... | ..... | ..... | ..... | ..... | 94.9 | 13,200 | 10,800 | 2,160 | ..... |

[1] Steer had 11 to 13 kg. hay per day, Nov. 27 to Dec. 2, inclusive; on Dec. 3 had 5.4 kg. hay.
[2] Weight on Dec. 2; not weighed on Dec. 4.
[3] Steer had about 9 kg. hay per day, Dec. 5 to May 4, inclusive, except when evening feed was withheld because of respiration experiment.
[4] Steer had 9.4 kg. hay May 5 and 4.7 kg. May 6.
[5] Steer had 13.3 kg. hay May 10; 13.2 kg. hay May 11; 12.6 kg. hay May 12; 13.1 kg. hay and 1.1 kg. grain May 13; on May 14 no hay given, but steer finished eating hay not eaten on May 13 and also had 2.3 kg. grain.

basis of per 500 kg. of body-weight the heat-production averages 9,100 calories per 24 hours. The series of low values during February and the early part of March are quite in accord with those noted with steers 2 and 4. During the period of realimentation, although the total heat-production increases very markedly, reaching as high as 14,800 calories on two days, June 25 and July 12, this increase is accompanied by such an increase in body-weight that the actual increase in the heat-production per 500 kg. of body-weight is not very great, although the values are higher than those during the early spring.

After June 5 the average is not far from 11,200 calories per 500 kg. of body-weight, as compared with 9,100 calories or perhaps less during the winter. This difference in the metabolism at the two nutritive levels is even more noticeable when we consider the values for the heat-production per square meter of body-surface per 24 hours. Aside from the low period during February and March, at which time a minimum value of 1,370 calories per square meter is noted, the average heat-production per square meter of body-surface throughout the winter is not far from 1,800 calories. During the super-maintenance period in the last weeks of fattening, the values rise to 2,300 calories, a great increase indicating definitely a much higher nutritive plane.

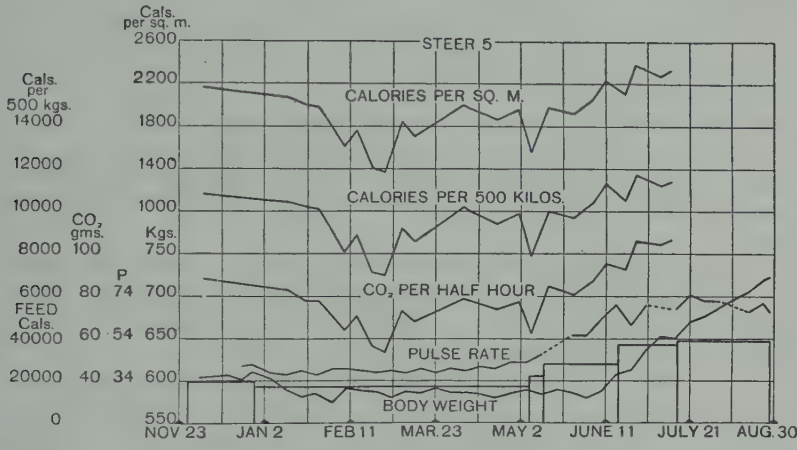


FIG. 27.—Curves for body-weight, pulse-rate per minute, carbon-dioxide production per half hour, and heat-production per 500 kg. of body-weight per 24 hours and per square meter of body-surface per 24 hours, and blocks for metabolizable energy in feed per day, steer 5.

## THE AVERAGE STANDARD METABOLISM OF STEERS 2, 4, AND 5, AS A GROUP, DURING MAINTENANCE AND SURFEIT FEEDING.

The series of experiments made throughout the winter on the three control steers of Group I (Nos. 2, 4, and 5) covered, we believe, the longest period of time thus far recorded in which normal animals have been fed a single, simple food material and the exact quantities actually consumed have been known. All three animals were presumably upon a ration slightly less than maintenance. We have reason to believe from subsequent experimental work (see p. 147) on steers A and B under similar condit ons of rationing at the start, that all the steers were losing more or less protein. To be sure, a complete balance experiment was not made with steers 2, 4, and 5, as the urine and feces were not collected. In the experiments with steers A and B, which showed a pronounced loss in protein, there was, however, a considerable restriction of activity and less exercise, since these two steers were kept in the stalls the entire time, were not allowed in the exercise lot, and were more or less in a condition of semi-hibernation. The evidence seems to be very clear, however, that steers 2, 4, and 5 were actually subsisting upon a ration somewhat less than maintenance. The genera condit on of the animals in Group I, using the body-weight as an index, remained uniform throughout

the hay period, and if we assume that the animals were on a maintenance ration, we have evidence as to the exact amount of hay of the quality fed that served to maintain three different steers for several months.

We likewise measured the metabolism a number of times throughout this period for purposes of comparison, noting considerable fluctuations in the carbon-dioxide production per half hour as well as in the computed heat-production, and these variations may be taken as representative of variations which will occur with normal animals under similar conditions of rationing. From the individual tables for the three animals, Tables 62, 63, and 64, it is seen that there are three distinctly different metabolic levels throughout the period of observation. On the first date or two, i. e., for the first experiments inside the respiration chamber, the metabolism values are relatively high, but, as has been seen from the previous discussion, they are quite in accordance with those noted with the 11 other steers in Groups II, III, and IV, which were studied under exactly the same conditions. Secondly, with all 3 animals the metabolism is exceptionally low some time during the winter, and finally, there is a striking increase in the metabolism during the period of realimentation, especially with steers 4 and 5, which were given heavy fattening rations.

Of these three different levels greatest stress must be laid, first, upon the general level during the period of hay maintenance, and secondly, upon the level during the period of fattening rations. It has been somewhat difficult to secure correct average results for the period of hay maintenance, since with all three animals a short period of very low metabolism was noted. In our consideration of the values during hay maintenance we have not eliminated this period of low metabolism, and hence in the subsequent table (Table 65, p. 246) we have recorded average values for the entire period of hay maintenance, although these averages do not represent the absolute minimum values found throughout the winter.

It is important to note, however, that even on a maintenance ration of hay only, the metabolism of these animals underwent a certain variation, as represented by the low level in the latter part of February and the early part of March, a low level which was experienced by all three animals alike. This low level of metabolism occurred in most cases at a period when the temperature of the environment was the lowest, and hence this fact of itself might be taken as an index that the lower environmental temperature actually lowered the normal, standard metabolism. In the light of practically all previous experimenting on this subject, however, it would be entirely erroneous to draw such a sweeping conclusion, and we shall content ourselves, therefore, at this stage by simply stating that this finding must be taken as directly opposite to the earlier conclusion regarding the influence of environmental temperature and, consequently, neither point of view can be considered as being thoroughly established.

We confess frankly that we are somewhat surprised that such a wide variation is to be found in the standard metabolism of normal animals. We were well acquainted with the variations to be found from hour to hour or half-hour to half-hour throughout the day, but the uniformity of the low values in February and March is striking, to say the least, and very difficult of explanation. Defective technique is, we believe, completely ruled out. Usually

it has not been considered as sufficiently established that there is a seasonal variation in metabolism. Our animals were, to be sure, stall-fed and considerably confined, and we might perhaps expect a repetition, in part at least, of the experience reported by Lusk[a] with a dog, which, after being confined to the laboratory for many months and subsequently being allowed to run in the country, showed an increase in metabolism of about 21 per cent immediately after the return from the country, although the body-weight remained constant. With humans an observation somewhat similar to that with our steers was noted with a squad of 12 men, Squad B, from the International Y. M. C. A. College at Springfield, Massachusetts.[b] With these men it was observed that there was a decrease in metabolism as the fall and winter went on, and that the last observation prior to their diet restriction was measurably lower than the first. This decrease in metabolism could by no means be ascribed to the greater familiarity of the men with the experimental procedure. It would appear as if with these steers the fact is clearly established that metabolic rhythm may be associated with the seasonal changes. In view of a finding such as this we consider it of particular value that we engaged in the expense and labor of maintaining this control group of animals. Without the data on this group our other findings would be extremely complicated. With such data we have a very much better measure of the true variations normally to be expected under identical experimental conditions, where the only factor altered is that of the quantity of the ration, which was curtailed for the other groups.

At this point it may again be emphasized that the pulse-rate data, as indicated on the charts and tables, confirm us in our view that during the period of realimentation the animals in Group I were living upon an essentially higher nutritive plane with a very much greater metabolic activity, for the pulse-rate increases with all three animals as the metabolism increases. On the other hand, it may be argued that during the period of lowest metabolic activity, namely, during February and March, the pulse-rate is not lowered, and this may be taken as proof that we have to deal here not with a true lowering of metabolism, but possibly with some experimental defect. While we are quite inclined to lay great emphasis upon the correlation between pulse-rate and metabolic activity, a point that has been stressed repeatedly in publications from the Nutrition Laboratory, it is clear that we may not use the pulse-rate data to buttress metabolism figures when the animal is on a high nutritive plane unless we also consider them seriously when the animal is on a lower nutritive plane. Examining for the moment the pulse-records secured with the Y. M. C. A. students on a low nutritive plane, we find that with all the men the curve for the pulse-rate when they were lying in the morning without food almost exactly parallels the curve for the basal heat-production, either the total heat-production per 24 hours or that per kilogram of body-weight or per square meter of body-surface per 24 hours.[c] In view of this finding, the explanation of the low heat-production of steers 2, 4, and 5 during February and March remains extremely complicated and to us quite unsatisfactory.

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[a] Lusk, Journ. Biol. Chem., 1915, 20, p. 565.
[b] Benedict, Miles, Roth, and Smith, Carnegie Inst. Wash. Pub. No. 280, 1919, pp. 495 et seq.
[c] *Ibid.*, fig. 124, p. 688.

Passing now to a consideration of the metabolism in the period of hay maintenance and subsequently in the period of surfeit feeding, we can use the general averages reported in the individual Tables 62, 63, and 64, for the 3 animals of Group I. Since it is somewhat difficult to make direct comparisons from the averages on the different tables, we have incorporated in Table 65 the average values found for steers 2, 4, and 5 on hay maintenance and for steers 4 and 5 also during the surfeit-feeding period. Steer 2 was turned out to pasture and not given grain, and hence no average value is available for him during surfeit feeding. At the very beginning one may fairly question the use of the average values as incorporated in Table 65, particularly those

TABLE 65.—*Comparison of the standard heat-production in periods of hay maintenance and surfeit feeding with hay and grain, Group I.*[1]

| Period. | Steer No.[2] | Average body-weight. | Heat (computed) per 24 hours. | | |
|---|---|---|---|---|---|
| | | | Total. | Per 500 kg. | Per sq. meter. |
| | | *kg.* | *cal.* | *cal.* | *cal.* |
| Hay maintenance[3] | 2 | [4]440 | 9,300 | 10,500 | 1,870 |
| | 4 | [4]496 | 9,600 | 9,700 | 1,800 |
| | 5 | [4]585 | 10,600 | 9,100 | 1,800 |
| Av., steers 2, 4, 5 | ..... | 507 | 9,800 | 9,800 | 1,820 |
| Av., steers 4 and 5 | ..... | 541 | 10,100 | 9,400 | 1,800 |
| Surfeit feeding[5] | 4 | [6]558 | 11,900 | 11,400 | 2,160 |
| | 5 | [6]648 | 13,200 | 10,800 | 2,160 |
| Av., steers 4 and 5 | ..... | 603 | 12,600 | 11,100 | 2,160 |
| P. ct. increase over maintenance (Av., steers 4 and 5) | ..... | 11.5 | 24.8 | 18.1 | 20.0 |

[1] Average values, based on data given in Tables 62, 63, and 64.

[2] Steer 2 was 2 yrs. 8 mos. old; steer 4, 3 yrs. 8 mos.; and steer 5, 4 yrs. 8 mos.

[3] Exclusive of December value.

[4] Average body-weight, Jan. 20 to May 10, inclusive, for steer 2; Jan. 8 to May 8, inclusive, for steer 4; and Jan. 13 to May 7, inclusive, for steer 5.

[5] Represents data secured between May 15 and July 12, 1919.

[6] Not an average body-weight for the entire period of surfeit feeding, but the final body-weight on July 12, the date of the last respiration experiment.

for the period of surfeit feeding. While the average values for the heat-production per 24 hours during the period of hay maintenance are not open to such serious criticism, since they are made up of reasonably uniform individual records, the general averages found with steers 4 and 5 for the period of surfeit feeding are quite deceptive in that they do not show the distinct tendency for high values during the last four or five observations, particularly in the heat-production per square meter of body-surface. Thus, the average value with steer 5 for the period of surfeit feeding, namely, 2,160 calories per square meter of body-surface per 24 hours, is measurably lower than the last three individual values (reported in Table 64) of 2,390, 2,280, and 2,330 calories, respectively. The same may be said with regard to the average value for the total heat-production and, indeed, for the heat-production per 500 kg.

of body-weight. If we were to select more particularly values preeminently characteristic of the period of surfeit feeding with steer 5, perhaps we should have used averages not for the entire realimentation period but for the period from June 20 to July 12, which would indicate a measurably higher metabolic level. Since we are dealing, however, not with the basal metabolism but with the standard metabolism, and since the general line of argument is not, we believe, affected by the use of the general average rather than the average on the high level, we are going to use for purposes of comparison the general average during the period of surfeit feeding as compared with the general average during the period of hay maintenance.

The average body-weights of these animals varied considerably, steer 2 being the youngest and also having the lowest body-weight, steer 4 being the next oldest animal and having the next highest body-weight, and steer 5, the oldest animal, having the heaviest body-weight. Considering, first, the values for the maintenance period, we observe that the total calories per 24 hours are greater with the larger body-weight, and hence the necessity for some direct method of comparison is obvious. When the heat-production is computed per 500 kg. of body-weight, on the other hand, the condition is exactly the reverse, for we have the largest heat-production per 500 kg. (10,500 calories) with the smallest, youngest animal, steer 2, and the smallest heat-production (9,100 calories) with the largest and oldest animal, steer 5. It is possible that the older, heavier animals give lower values per 500 kg. of body-weight. Whether we have to do here with a specifically higher metabolism of the young in the case of steer 2, and with the addition of inert fat in the case of steer 5, combined with the age factor to lower the metabolism per 500 kg., it is at this point not possible to state. The average heat-output for all three animals is 9,800 calories, which may be taken as the standard metabolism per 500 kg. of body-weight of stall-fed, quiet steers, 24 hours after the last meal, the ration consisting exclusively of hay in an amount presumably sufficient for maintenance, so far as body-weight is concerned.

On the basis of equal surface-area, the highest average value is noted with the youngest animal, steer 2, i. e., 1,870 calories, while with steers 4 and 5 the same value is found, namely, 1,800 calories. With these three steers, therefore, the grosser differences exhibited in the heat-production per 500 kg. of body-weight are partly wiped out when the computation is made per unit of surface area. The extreme percentage variation between 9,100 calories and 10,500 calories per 500 kg. of body-weight, amounting to about 14 per cent, is reduced, when the comparison is made on the basis of surface-area, to about only 4 per cent, i. e., a range of 1,800 to 1,870 calories. It is thus clearly demonstrated that for the comparison of steers retained under equal conditions with regard to environment, feed, and activity, an average value throughout the winter is more closely obtained from the heat-production per square meter of body-surface than from that per 500 kg. of body-weight or from the total heat-production per 24 hours.

Before laying too much stress upon this rather significant fact, however, one must recall that with the same animal, particularly during the period of hay maintenance, the heat-production per square meter of body-surface (as is seen in the individual Tables 62, 63, and 64) undergoes tremendous variations throughout the winter, variations which have already been emphasized.

Thus, steer 4 had a range in the heat-production per square meter of body-surface from 1,250 calories on March 12 to 2,140 calories on January 8; steer 5, from 1,370 calories on February 27 to 2,070 calories on January 13; and steer 2, from 1,480 calories on February 19 to 2,600 calories on January 8. The lower value in all three instances occurs in the period of extraordinarily low metabolism observed with all three animals. In view of this fact, it is obvious that any average value must be used with considerable reserve. However, the grand average value of 1,820 calories per square meter of body-surface does suffice for a general comparison of the three different animals, but it has absolutely no significance as an indication of the true standard metabolism of a given animal at any given period throughout the year.

Since only steers 4 and 5 received surfeit feeding, the grand averages for the period of hay maintenance are given not only for all three steers together, but likewise for steers 4 and 5, alone, for subsequent comparison with their grand averages obtained during the fattening period. It is to be observed that in the maintenance period the difference between the grand averages for all three steers and the grand averages for steers 4 and 5 is not appreciable. With animals varying in weight as much as these animals did, the general average figure for all three steers of 9,800 calories for the total heat-production per 24 hours has perhaps not very great significance. In the period of surfeit feeding there is not only a considerable increase in the body-weight, but particularly in the heat-production on all bases of computation, increases indicating a very much higher metabolic level for steers 4 and 5 during the fattening period.

What is specially emphasized, not only by Table 65 but particularly by the individual Tables 62, 63, and 64, is the fact that there is a remarkably different metabolic level throughout the period of hay maintenance as compared with the period of realimentation with hay and grain, and that even during the maintenance period there are wide variations in the heat-production per square meter of body-surface, particularly at the low level in February and March. From the evidence secured with these three control steers, therefore, we have proof of the existence of at least two definite nutritive planes in the course of the experimental year, entirely separate from each other. Furthermore, we have proof that during the maintenance period there is a decreasing nutritive plane from the initial standard to a relatively low level about the latter part of February with all three animals, with a tendency for the nutritive level to increase thereafter until the end of this period, followed (at least so far as the two steers subjected to fattening rations, Nos. 4 and 5, are concerned) by a rather rapid, striking increase at the beginning of the grain period and later by a steady increase as the fattening period progresses. The evidence with regard to steer 2 on pasture is confined to but one experiment, and therefore does not lend itself to discussion.

From these normal control data, then, we are to conclude that on a constant maintenance ration of mixed hay alone, under constant conditions of stall-feeding, activity, and general treatment, the control steers passed through several months with marked changes in their standard metabolism, and, since all three animals give the same picture of a lowered metabolism during the latter part of February and March, the evidence seems to be conclusive that we have here an extraneous factor, exclusive of the ration itself, probably temperature or season, a factor profoundly affecting the metabolic level of

these animals. Hence it is impossible to state what is the normal, standard metabolism of a normal animal and expect it to hold inflexibly throughout an entire year, even with constant ration, with constant body-weight, and with constant stall activity. What would be the condition were the factors of climate and temperature controllable it is difficult to state. With the large number and geographical distribution of experiment stations in the United States, and with the variations in climate, it is to be hoped that tests of this kind may be carried out on animals where more uniform, regular climatic conditions obtain and where the seasonal variations are not so great as they are in northern latitudes, as experiments of this type would throw much light upon this important problem. Obviously such tests have a great bearing upon the nutrition of animals in barns or in open lots, and hence are not without practical significance.

The figures in Table 65 show quite conclusively the inexpediency of attempting to compare the total heat-production of animals of varying age and weight

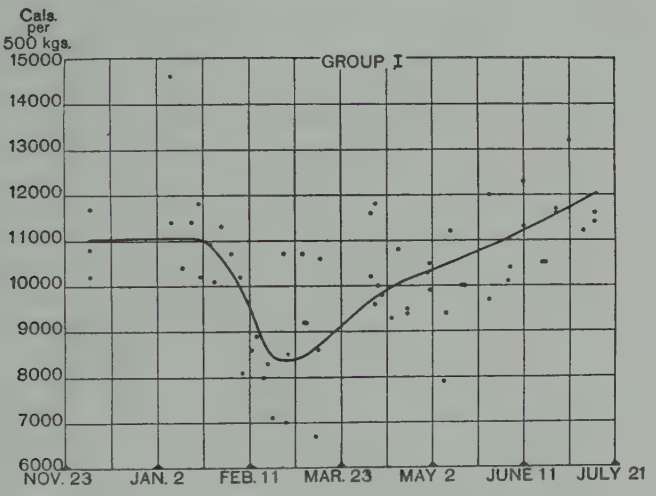


FIG. 28.—Curve showing the general trend of the standard heat-production per 500 kg. of body-weight per 24 hours, Group I.

without making any allowance whatsoever for differences in size. In this table only average values are considered, and these indicate clearly that there are two distinct metabolic levels, one on the maintenance ration of hay and one on the heavy grain ration. The fact that there is a very low level in February and March is not brought out in this table, but is shown in the individual tables and charts. To study more critically the general, average trend of the metabolism of these animals during the winter, we have considered it advisable to plot on one chart (Fig. 28) all the data available for Group I for the heat-production per 500 kg. of body-weight[a] and through the plotted points we have sketched roughly a curve representing the general trend of the metabolism. This curve, as is customary with curves of this kind drawn at the Nutrition Laboratory, is the resultant of the independent impression of five

[a] In Figs. 28 and 29 the data for steer 2 were plotted only up to May 20, as thereafter he was not fed on hay and grain, as were steers 4 and 5, but was put on pasture.

skilled workers with charts and curves, and while not laid on with mathematical accuracy, it does indicate very closely the general metabolic trend in so far as the trend for such widely divergent points can be true.

In general, the heat-production per 500 kg. of body-weight remains essentially constant for the first month and a half, and then steadily falls off until about the first of March when a minimum point is reached. After this date there is a steady increase, the rate of increase being uniform even through the fattening period. Confining our attention only to the so-called "maintenance" period with hay, we find that there is a variation in the heat-production per 500 kg. of body-weight from a level of 11,000 calories at the start to a level of 8,400 calories on the first of March. Since this is a composite curve based on the data for all three animals, further proof of an absolute change in metabolic level could hardly be asked for. The maximum heat-production reached at the end of the experimental season about the middle of July is 12,000 calories per 500 kg. of body-weight.

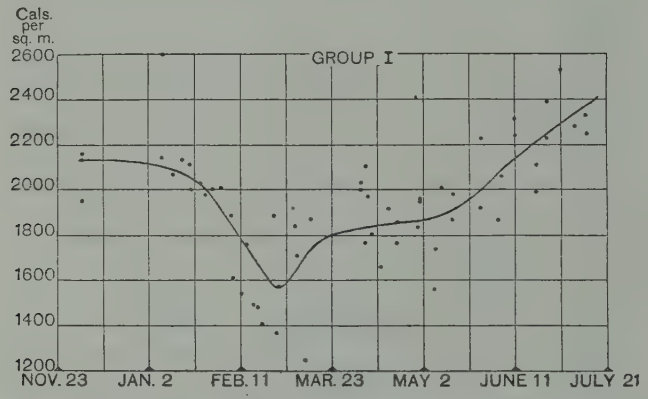


FIG. 29.—Curve showing the general trend of the standard heat-production per square meter of body-surface per 24 hours, Group I.

The computation of the heat-production per square meter of body-surface is considered by practically all writers in animal nutrition as a somewhat more satisfactory basis for the comparison of different animals than that per unit of body-weight. It is of interest, therefore, to examine the data as presented in Fig. 29, in which the individual values for all of our experiments computed on the basis of per square meter of body-surface are plotted. Here again a line was sketched through the plotted points representing the most probable trend of the metabolism throughout the year. The curve is strikingly similar to that in Fig. 28, indicating a level at about 2,120 calories per square meter of body-surface per 24 hours for about a month and a half and thereafter a distinct fall, with a minimum of 1,570 calories not far from the first of March, with steadily increasing values from there on. However, it is easily seen from the wide scatter of points on a curve of this kind that the general trend of the curve can be drawn only with the greatest degree of conservatism and must not in any sense be considered as an exact mathematical expression of the regularity in the heat production of these animals at different times of the

year. Figs. 28 and 29 do serve, however, to visualize the tremendous variation in the normal, standard metabolism, even when the heat-production is computed by the two best accepted methods for equalizing all animals, namely, per unit of body-weight and per unit of body-surface.

Having noted clearly the wide fluctuations in the heat-production per unit of body-weight and per unit of body-surface, as shown in Figs. 28 and 29, we can return again to a consideration of the average values in Table 65 for the maintenance period and for the realimentation period, average values which naturally wipe out many of the wide fluctuations existing in the two periods, particularly in the maintenance period. From Table 65 it is seen that during the period of hay maintenance, the average total heat-production was 9,800 calories for all three animals, the heat-production per 500 kg. of body-weight was 9,800 calories, and that per square meter of body-surface 1,820 calories. A slightly different average for steers 4 and 5 (omitting steer 2) is best used for comparison with the averages found for the fattening period. It is important to note that steers 4 and 5 had not made *very* heavy increases in weight during the so-called "fattening" period, steer 4 changing from an average maintenance weight of 496 kg. to a final weight in the fattening period of 558 kg., an increase of 12.5 per cent, while steer 5 increased from 585 kg. during the maintenance period, to 648 kg. during the fattening period, or only 10.8 per cent. However, as compared with the standard length of fattening periods in economic practice, that of steers 4 and 5 was relatively short, being only 107 days. At this point we should observe how the increases in standard metabolism compare with these increases in body-weight. Leaving out of consideration entirely the total heat-production, and confining ourselves to the two methods for equalizing animals of different size, we find that with steers 4 and 5 the heat-production per 500 kg. of body-weight increases on the average 18.1 per cent, as compared with an average increase in body-weight of 11.5 per cent. Furthermore, the heat-production computed per square meter of body-surface shows an increase in these two animals of 20 per cent over that during the maintenance period. Finally, if the last three individual metabolism measurements in the fattening period (as reported in Tables 62, 63, and 64) are used as standards, in each case the percentage increase in metabolism becomes even greater.

Such increases in the standard heat-production at the two different nutritive levels recall the interesting observations of Armsby and Fries,[a] in which they found that an unfattened steer, weighing on the average 513 kg. in the unfattened state, had a daily heat-production per 1,000 pounds of live weight, in proportion to the two-thirds power of the weight, of 5,125 calories, while the same steer, when fattened and weighing 649 kg., had on the same basis a daily heat-production of 5,943 calories. In this particular case, however, the animal actually increased 27 per cent in weight over the unfattened state, while the percentage increase in the total metabolism was 36 per cent, and the increase on the basis of the two-thirds power of 1,000 pounds of body-weight was about 16 per cent. By their method of computation they find an increase of 16 per cent in the heat-production as against an increase in body-weight of 27 per cent, and they state that apparently the accumulation of fat tended to stimulate the general metabolism. With our own particular ani-

[a] Armsby and Fries, Journ. Agric. Research, 1917, 11, p. 461.

mals, as shown in Table 65, the increase in body-weight amounted to but 11.5 per cent, while there was an increase in the total heat-production of 24.8 per cent, in the heat-production per 500 kg. of body-weight of 18.1 per cent, and in the heat-production per square meter of body-surface of 20 per cent. Our animals were not fattened to the degree that the steer of Armsby and Fries was, and both in the maintenance and the so-called "fattening" period they were very much nearer a uniform state than was the steer of Armsby and Fries.

### COMPARISON OF OUR NORMAL STANDARD METABOLISM DATA WITH BASAL METABOLISM DATA SECURED BY ARMSBY.

Because of the divergence in the standard metabolism measurements shown in Figs. 25 to 27, and particularly in the composite curves in Figs. 28 and 29, which indicate clearly several nutritive planes, it is very difficult to conceive of a normal standard metabolism that will apply to all seasons of the year, even with steers on a uniform feed-level. At the beginning of the year the heat-production per 500 kg. per 24 hours was, on the average for Group I, approximately 11,000 calories, a value which is very close to the average value found for all 14 steers (11,300 calories) in the first observation of the year (see Table 61, p. 231). On the basis of the heat-production per square meter of body-surface during the first part of the year, the average value for Group I was 2,120 calories, which again is almost identical with the grand average for the 14 steers studied on the first date of the year. But the minimum heat-production for the three steers of approximately 1,570 calories per square meter of body-surface at the low point of the curve, followed by very considerable increases due to fattening, makes the assumption of any general, average, normal standard very questionable. Considering only the general metabolism, when the animals in Group I were in the most uniform condition and when they had been for the longest continuous period of time upon a uniform feed-level, namely, during the period of hay maintenance, we have accepted the average value for all three animals of 1,820 calories per square meter of body-surface per 24 hours. This value, however, does not indicate the high results obtained on the first days of experimenting, nor, indeed, the extremely low values in February and March, mentioned above, but represents simply an average. Nevertheless, it may be taken in general as an average measurement representing the same period of time as covered by the period of low rationing of the other animals. This value of 1,820 calories per square meter of body-surface represents, then, our measurement of the normal, standard metabolism of an animal 24 hours after the last feed, during a period when he is subsisting upon mixed hay in sufficient amount to maintain approximate constancy in weight. May this value be taken as the normal, standard metabolism of an adult steer? It is apparent from the analysis of the results obtained in the first experiment with each of 14 steers that this value may not be so accepted, as it is some 320 calories, or nearly 15 per cent, less than the average value of 2,140 calories found for the 14 steers. But it has already been admitted that in all probability this initial value of 2,140 calories was somewhat high, owing to some excitement of the animals during their first experiments, due to the novelty of the situation, and owing to the possible differences in pre-experimental feed conditions.

How does this average value of 1,820 calories compare with commonly accepted estimates of the so-called "basal metabolism"? A most careful estimate of the so-called "basal metabolism" of steers and their comparison with that of other species has been made by Armsby, Fries, and Braman.[a] These authors employed the conventional method of computing the basal metabolism of ruminants by studying the animal under conditions where two rather widely varying amounts of the same feed were given. They noted the influence of the difference in the weight of feed upon the heat-production, and, assuming that the heat-production caused by the feed is a linear function of its amount, they deducted from the measured heat-production that proportional amount due to the feed and considered that the difference represented the basal metabolism. Upon the basis of this long-established custom, they secured values in 27 experiments with 10 different steers, studying the effect of quite a wide variety of feeds, including a number of experiments on timothy hay alone. Their data have been computed on the basis of the basal metabolism with the animal lying 24 hours, standing 12 hours out of the 24 hours, and standing 24 hours. Obviously, for comparison with our own results, only the computation on this latter basis is permissible, since our animals were invariably standing the entire time. Armsby, Fries, and Braman find as a mean of all their experiments that when the animal is standing for 24 hours the basal katabolism per square meter of body-surface is 1,365 calories. It is important to note that these computations are based also upon Moulton's improved factors and formulæ for computing the surface-area of cattle.

This value of 1,365 calories is noticeably lower (455 calories) than the average value of 1,820 calories for steers 2, 4, and 5 reported by us in Table 65. That the values of Armsby, Fries, and Braman are measurably lower throughout the entire series than those noted by us is made clear by reference to the next to the last column of Tables 62, 63, and 64, in which it can be seen that of the 41 values involved in the averages for these 3 animals on hay maintenance, there are but 2 which are as low as the Armsby average of 1,365 calories, namely, 1,250 calories with steer 4 on March 12 and 1,370 calories with steer 5 on February 27.

The average difference of 455 calories per square meter of body-surface is very difficult to explain. In their comparison of the basal metabolism of their cattle with those of other species Armsby, Fries, and Braman have properly laid weight upon those computations made when the animal was lying, but for our special purpose we must obviously confine ourselves to the computations for the 24-hour standing experiments. To our mind the legitimacy of this method of computing the basal metabolism, which has been employed in general by workers in animal nutrition, may be questioned. When animals consume different amounts of feed, differences in the effect of the feed enter extensively into the computations. In our case our animals had been without feed for 24 hours. Undoubtedly our measurement did not represent basal metabolism. It is possible that the metabolism as measured by us was 455 calories above the basal metabolism per square meter of body-surface. Hence the difference between our values and Armsby's values may be taken by the adverse critic as a proof that the digestive condition of our animals was

[a] Armsby, Fries, and Braman, Journ. Agric. Research, 1918, 13, p. 43; *ibid.*, Proc. Nat. Acad. Sci., 1918, 4, p. 1.

measurably above the basal state, and that since the older method of computation gives distinctly lower values, and since these lower values apparently agree with wonderful concordance with the basal metabolism of other species, in all probability the values found by us for standard metabolism are very much higher than those for basal metabolism.

In connection with the valuation of our *standard* metabolism results, we have already considered the factors that affect basal metabolism. They are of course primarily the digestion of feed and muscular activity. Of these two, muscular activity can practically be ruled out, for certainly in Armsby's experiments there would have been essentially the same degree of activity as with our animals, indeed probably somewhat more, since in addition to the metabolism during standing his values include that required for eating and ruminating, which was not included under the conditions of our experiments. However, the matter of the digestion of feed is presumably, by the method of computation used by Armsby and other writers in animal nutrition, ruled out. The difficulties of measuring directly the basal metabolism of ruminants with large masses of fill have already been stressed. The point at issue now is as to whether our *standard* metabolism includes a large proportion due to the active processes of digestion or the after-effects of active digestive processes.

The difference between our standard metabolism value of 1,820 calories per square meter of body-surface per 24 hours and Armsby's value of 1,365 calories amounts to 455 calories, which is an increment over Armsby's value of 33 per cent. If it could be shown that under our conditions of standard metabolism there was an increase in metabolism of 33 per cent represented by *digestive* activity, then the discrepancy between the two series would be entirely wiped out. That there is undoubtedly some increased metabolism due to an after-effect of digestion, and that we have not true *basal* metabolism is not for one instant denied. But that there can be an increase amounting to 33 per cent seems improbable, for, in the first place, it will be recalled that even in our experiments where excessive muscular activity and extreme restlessness obtained, we seldom found an increase equivalent to 33 per cent. To prove this point, however, an experiment when the animal had been longer than 24 hours without feed would be essential. We have already discussed in some detail our own values representing experiments made later than 24 hours after the withdrawal of feed. We have shown that it is true in general that there is a still further decrease in metabolism at the end of 48 hours over that at the end of 24 hours after feed. In most instances, however, the comparisons are unfortunate in that the experiments usually were not made under comparable conditions as regards activity.

Reference must be made to the original discussion on pages 209 to 215, where we analyzed the data in Tables 55 and 57. At that point we were particularly interested in the fundamental question as to how accurately the production of carbon dioxide represents standard metabolism, not basal metabolism. Consequently, we included all of the experiments that we had on this subject, made at either of the two nutritive planes on which these animals were living at different times. Our present discussion, it is to be remembered, deals only with the question of the nutritive plane during maintenance feeding, at which level we found a standard metabolism per square meter of body-surface per 24 hours of 1,820 calories as an average for 3 animals. This average is at the

moment being compared with the low value recorded by Armsby and his associates of 1,365 calories for the basal metabolism, standing. For this special purpose it is desirable to refer to Tables 55 and 57 (see pp. 210 and 213), considering only those experiments made during periods of hay maintenance and after rather prolonged withdrawal of feed. In Table 55 there are only two experiments during hay maintenance, i. e., with steer 10 on May 8 to 9, and with steer 4 on May 8 to 9. In both cases a small decrease in the metabolism is noted as the fast progresses and with both steers the decrease amounts to approximately 10 per cent. In Table 57 there are two comparable results obtained on January 7 to 8, with steers A and B during the period of hay maintenance. Both experiments show a decrease in metabolism as the fast progresses, approximately 10 per cent in the case of steer A and nearer 20 per cent in the case of steer B. Of all the experiments made throughout this period of hay maintenance, therefore, only one, that with steer B, may be taken as indicating a large decrease in metabolism as measured by the carbon-dioxide production 53 hours after feed as compared with that 29 hours after feed. In all the other cases the decrease is about 10 per cent.

While our own data, as recorded in Tables 55 and 57, suggest a decrease of about 10 per cent in the carbon-dioxide production at the forty-eighth hour as compared with the twenty-fourth hour after feed, a slight correction for the difference in the calorific value of carbon dioxide would make this decrease not quite so great. This correction we have not made, however. Fortunately, we may refer to the details of the experiments kindly put in our hands by Professor Armsby. Some experiments of Professor Armsby, made upon two fasting cows, included the direct measurement of the heat-production and the carbon-dioxide production in two consecutive 24-hour periods during approximately maintenance feeding and two consecutive 24-hour periods after 24 hours of fasting. Both cows received the same experimental treatment. The details of the experiments (as communicated to us by Professor Armsby with permission to use them) are given in Table 66. Although these experiments were called to our attention primarily as an aid to the determination of the suitable calorific value of carbon dioxide to use in our tests and have been discussed *in extenso* in an earlier section of this report (see p. 206), special emphasis is here given to the carbon-dioxide production and heat-production in the periods following 24 hours of fasting.

During maintenance feeding the carbon-dioxide production per 24 hours was, on the average for 2 days, 3,675 grams with cow No. 885 and 3,384 grams with cow No. 886. In the first 24 hours after 24 hours of fasting, the carbon-dioxide production drops to 2,208 grams with cow No. 885, and 2,185 grams with cow No. 886. This drop is not surprising, in view of the fact that in the first instance the animals were studied at the height of digestion and with the activity incidental to the mechanical work of digestion and rumination. During the second 24 hours after 24 hours of fasting the drop in the carbon-dioxide production is inappreciable in both cases, i. e., a drop from 2,208 grams to 2,111 grams with cow No. 885 and a larger drop from 2,185 grams to 1,964 grams with cow No. 886.

Our own measurements obviously deal with the first 12 hours of the first 24 hours following 24 hours of fasting. Professor Armsby and Professor Braman have kindly sent us their data for these individual periods, which are also

incorporated in Table 66, the values in parenthesis representing our computations of their data on the 24-hour basis for purposes of comparison. Admitting for the moment that the carbon-dioxide production in the first 24 hours after 24 hours of fasting represents an approximately basal metabolism, we see that in the case of cow No. 885 for the first 12 hours of this time the carbon-dioxide production is but 4.3 per cent higher than that for the entire 24 hours, i. e., 2,304 grams as against 2,208 grams, while with cow No. 886 it is only 2.9 per cent higher, i. e., 2,248 grams as against 2,185 grams. Comparing the first 12 hours of the first 24 hours after fasting with the second 24 hours after fasting, we find that the results are on the average 12 per cent

TABLE 66.—*Results obtained in experiments with fasting cows.* (*Armsby.*)

| Cow and average body-weight. | Period of observation. | Average daily feed per kg. body-weight.[1] | Heat production. | Carbon-dioxide production. | $CO_2$ to heat ratio. |
|---|---|---|---|---|---|
| | | *gm.* | *cal.* | *gm.* | |
| Cow 885, 425.5 kg... | Period III, approximate maintenance.. | 10.45 | ..... | ..... | ..... |
| | First 24 hours..... | ..... | 8,762 | 3,699 | 2.369 |
| | Second 24 hours..... | ..... | 8,938 | 3,650 | 2.449 |
| | Average..... | ..... | 8,850 | 3,675 | 2.409 |
| | Period IV, after 24 hours fasting: | | | | |
| | First 24 hours..... | ..... | 6,814 | 2,208 | 3.086 |
| | First 12 hours of first 24 hours.... | ..... | [2]3,575 | 1,152 (2,304) | 3.103 |
| | Second 24 hours..... | ..... | 6,642 | 2,111 | 3.146 |
| Cow 886, 419.5 kg... | Period III, approximate maintenance.. | 10.39 | ..... | ..... | ..... |
| | First 24 hours..... | ..... | 7,889 | 3,360 | 2.348 |
| | Second 24 hours..... | ..... | 7,989 | 3,407 | 2.330 |
| | Average..... | ..... | 7,939 | 3,384 | 2.339 |
| | Period IV, after 24 hours fasting: | | | | |
| | First 24 hours..... | ..... | 6,874 | 2,185 | 3.146 |
| | First 12 hours of first 24 hours.... | ..... | [2]3,458 | 1,124 (2,248) | 3.077 |
| | Second 24 hours..... | ..... | 6,391 | 1,964 | 3.254 |

[1] The feed, which was the same in periods III and IV, consisted of a mixture of alfalfa hay, maize meal, ground oats, wheat bran, and linseed meal. The same amount of this feed mixture was fed to the cows each day for a period of approximately 2 months before the beginning of the observations.

[2] These two figures were supplied to us with the statement that they might later be subject to a very minor correction.

higher in each case, that is, the carbon-dioxide production in the first 12 hours after a 24-hour fast is about 12 per cent greater than it is during the second 24 hours after a 24-hour fast.

If we can consider the possibility of the fasting metabolism approaching basal in the second 24 hours after a 24-hour fast, we shall be much nearer the true basal metabolism. It will be recalled that in this entire discussion we are considering only the influence of previously ingested food upon basal metabolism, and strictly speaking, not basal metabolism but basal metabolism standing. Have the processes of digestion practically ceased in the second 24 hours after 24 hours of fasting? Our answer to this is fortunately again due to the admirable researches of Professor Armsby and to his characteristic generosity in placing the tentative figures in our hands. Based upon the

measurement of the methane excretion, which may be taken as an index of the digestive and fermentative activity, Professor Armsby finds that after 72 hours of fasting the amount of methane is very small and remains constant until 144 hours or more of fasting, beyond which his experiments did not extend. It may, therefore, be inferred that digestive activity has practically ceased by the end of the second 24 hours after 24 hours of fasting. Since from Professor Armsby's own figures the carbon-dioxide production during the first 12 hours after 24 hours of fasting is but 12 per cent above the carbon-dioxide production for the second 24 hours after 24 hours of fasting, it can be seen that our values for heat-production (computed from the carbon-dioxide production) obtained during the first 12 hours after 24 hours of fasting can not in all probability be any greater than 12 per cent above the basal metabolism, on the assumption that the metabolism has reached basal during the second 24 hours after 24 hours of fasting.

It is to be remembered that our computed value for the standard metabolism, standing, is approximately 33 per cent higher than that given by Armsby and his associates for the basal metabolism standing. That is, we find on the average 1,820 calories per square meter of body-surface per 24 hours, while they report 1,365 calories. From our analysis of our own figures, and particularly those of Professor Armsby, it seems incredible that our standard metabolism, standing, can be much more than 12 per cent (if, indeed that much) above the true basal metabolism, standing. That being the case, the only inference is that the basal values computed by Professor Armsby and his associates and, indeed, the entire method of computing the basal metabolism by making experiments during the ingestion of feed, with two different amounts of feed, are seriously to be questioned. The discrepancy between the two standards for standing metabolism is so great, 33 per cent, that it is very difficult to obtain any light upon this subject. If, for example, we consider not the carbon-dioxide production but the heat-production of Professor Armsby's cows, we find that the heat-production per 24 hours averages for both animals, 8,395 calories during 2 days on approximate maintenance, 6,844 calories for the first 24 hours after 24 hours of fasting, and 6,517 calories for the second 24 hours. The difference between the daily heat-production on approximate maintenance, 8,395 calories, and that in the second 24 hours after 24 hours of fasting, 6,517 calories, is 1,878 calories. That is, the heat-production on the maintenance ration is 28.8 per cent above that during the second 24 hours after 24 hours of fasting. In other words, had our standard measurements been made during full feeding and Professor Armsby's basal metabolism measurements made during the second 24 hours after 24 hours of fasting, the difference in the measurement of metabolism, i. e., 28.8 per cent, would not be so great as is now represented by the two standards for the heat-production per square meter of body-surface, i. e., 33 per cent.

This suggests two very important points, first, as to the question which has been raised and with characteristic generosity raised by Professor Armsby himself in a letter received shortly before his untimely death, namely, that the whole method of computing the basal metabolism of ruminants is open to serious objection; secondly, if this method of computing the basal metabolism of ruminants is defective, as it seems to be from this analysis, it is futile to make the comparison of the basal metabolism of ruminants with those of

other species, particularly man, as has been so often done, and the universality of the surface-area law for warm-blooded creatures again receives a serious check. This is not the place to discuss the question of the basal metabolism of cattle as compared to that of humans. This comparison is of fundamental, physiological importance in the study of the heat-production and heat elimination of warm-blooded animals. Further experiments with fasting ruminants are in progress at the moment of writing, experiments not only in our respiration chamber at Durham, but also at the Institute of Animal Nutrition at State College, Pennsylvania, by Professors Fries and Braman, who are carrying out a posthumous experimental plan of Professor Armsby. Not until such experiments are completed will evidence be available for a more intelligent, thorough discussion of the probable basal metabolism of ruminants as compared with that of other species.

## THE STANDARDS OF REFERENCE FOR COMPARISON OF UNDERNOURISHED AND FULL-FED ANIMALS.

From the foregoing discussion it would appear as if there was no definite normal standard metabolism of ruminants, even with animals on a ration sufficient to maintain constancy in body-weight. Under the circumstances, therefore, it is particularly fortunate that we persisted in including a group of normal steers in our general study of undernutrition, for without some standard of reference we could not use the older values in any way, since, as shown in the preceding section, they have already been called into serious question. Irrespective of what is or what is not *basal* metabolism, we do have accurate measurements throughout the experimental year of the standard metabolism of a group of animals held at nearly constant weight. These measurements may be definitely used for standards of reference for the other groups of animals which were subjected to submaintenance rations, and hence our special data secured with Group I will be used as standards of reference, and no further consideration at the present time will be given to the normality of these results as compared with the results of earlier work.

The general curve (see Fig. 29, p. 250) representing the trend of the heat-production per square meter of body-surface per 24 hours for the 3 control steers shows clearly differences in metabolic level throughout the season (attention has already been called to at least three different levels), and it seems wise to attempt to secure figures which will represent approximately these differences in level. From the data in Table 61 (see p. 231), where the results are given for all 14 steers on their first day inside the respiration chamber, when they were presumably subsisting upon a maintenance ration of hay alone, it was found that the grand average value corresponded to 11,300 calories per 500 kg. of body-weight and 2,140 calories per square meter of body-surface. Strictly speaking, this latter value of 2,140 calories should be taken as the representative average value for steers on a maintenance ration of hay alone, rather than the average result obtained with the 3 control steers, Nos. 2, 4, and 5, for the 11 other animals were maintained at the start under identically the same conditions. For the subsequent phases of normal alimentation, that is, the low period in the early spring and the subsequent fattening period, however, it is necessary to use the values for Group I,

i. e., steers 2, 4, and 5. Consequently, in Table 67 is collected a series of average figures representing the heat-production per square meter of body-surface per 24 hours for these 3 animals on the four different nutritive planes: first, the actual initial values at the beginning of the maintenance period with hay, which correspond to the initial values for the 11 other animals; second, the average values throughout the period of hay maintenance, which automatically include certain very low values and hence are figures measurably lower than those obtained at the beginning; third, the average values for the low level of hay maintenance which, it will be recalled, was noted with all 3 animals; and finally, in the case of steers 4 and 5, the average values for the fattening period with hay and grain.

The last column of Table 67 gives the group averages. The general average of 1,820 calories for all 3 animals during the period of hay maintenance is made up of widely fluctuating values, including the low values which make up the separate general average of 1,470 calories obtained during the low level of hay maintenance. On the other hand, the average value of 2,160 calories

TABLE 67.—*Standard heat-production per square meter of body-surface per 24 hours on different planes of nutrition, Group I. (Average values.* [1])

| Plane of nutrition. | Steer 2. | Steer 4. | Steer 5. | Group average. |
|---|---|---|---|---|
| | *cal.* | *cal.* | *cal.* | *cal.* |
| Beginning hay maintenance[2]... | 2,130 | 1,950 | 2,160 | 2,080 |
| Hay maintenance[3]..... | 1,870 | 1,800 | 1,800 | 1,820 |
| Low level of hay maintenance[4]. | 1,510 | 1,500 | 1,390 | 1,470 |
| Fattening with hay and grain[5].. | ([6]) | 2,160 | 2,160 | 2,160 |
| Age..... | 2 yrs. 8 mos. | 3 yrs. 8 mos. | 4 yrs. 8 mos. | 3 yrs. 8 mos. |

[1] Based on data given in Tables 62, 63, and 64.
[2] Represents one value only, secured on Dec. 4, 1918.
[3] Exclusive of December value.
[4] Represents two to four values secured in late February.
[5] Represents data secured between May 15 and July 12, 1919.
[6] Steer 2 was not fattened on hay and grain, but put to pasture on May 20, after which date only one respiration experiment was made with him.

during the fattening period also represents a mean of widely varying values and does not give any indication of the maximum values actually reached at the end of the period of excess feeding, but represents only an average midway between the lower values at the start and the higher values at the end of this period. However, for a consideration of the general average trend of the standard metabolism and to secure certain standards of reference which may be applied to our animals that were subjected to curtailed rations, these general figures are employed. To these but one major correction should be applied. That is, we believe that instead of using for a standard of reference the average of 2,080 calories obtained from 3 steers at the beginning of the period of hay maintenance, it would be more logical to assume that the value of 2,140 calories obtained from all 14 animals (as shown in Table 61) would be more nearly representative of the true condition, and should therefore be applied as the probable factor for Group I. Employing this latter factor, 2,140 calories, we find that during the maintenance period the general

averages range from 2,140 calories to 1,470 calories at the lowest level of hay maintenance. Using 1,470 calories as a basis, it can be seen that 2,140 calories corresponds to an increase of nearly 50 per cent in the metabolism. It is also of importance to note that 2,140 calories is essentially that recorded as the mean for the fattening period with hay and grain rations, i. e., 2,160 calories, although, as pointed out above, the latter is a mean and does not represent the highest values in the very last stages of fattening, when both steer 4 and steer 5 showed values nearer 2,300 calories. It is quite likely that 2,160 calories does not represent the highest fattening level, which should be determined before intelligent use can be made of it for comparison of animals on fattening rations. However, our main problem is to consider the animals during the period of hay maintenance, and particularly on the low level of metabolism on hay maintenance.

That 3 animals on a presumably normal, uniform ration of hay and under otherwise reasonably constant conditions can exhibit such an average variation in metabolism, i. e., from 2,140 calories to 1,470 calories, is striking confirmation of the fact that there is no normal, standard metabolism of ruminants which may be used as an inflexible standard for general comparison. Attention again must be called to the fact that the low value of 1,470 calories at the low level of hay maintenance is but slightly greater than the value of 1,365 calories ascribed by Professor Armsby to the basal metabolism, standing. It is hardly to be supposed, however, that the nutritive plane at which our 3 animals were living during the latter part of February and the first of March is at all comparable to that obtaining with Professor Armsby's animals, all of which were living under maintenance conditions of full feed. In general, therefore, we may employ an average value of 2,140 calories for the standard heat-production per square meter of body-surface per 24 hours when our animals are on full feed, and a somewhat lower value of 1,820 calories for the prolonged period of hay maintenance, with the possibility of an actual minimum value of 1,470 calories representing seasonal variation on maintenance. The use of these isolated figures does, it is true, present a crude picture of the general trend of the metabolism, as shown by the curve in Fig. 29, but it is obvious that for any more exact comparisons the use of the curve is preferable.

### Metabolism as Affected by Pronounced Curtailment in Ration.

Whatever of interest the metabolism measurements on our control steers may have (and the study of these animals has definitely shown hitherto unsuspected changes in metabolic level throughout the winter), the main purpose of this inquiry was a study of the influence of curtailed rations upon the live weight and the physiological activities of these large ruminants. A careful study is, therefore, necessary of the results obtained upon the three groups of animals subjected to ration curtailment, Groups II, III, and IV. Since these groups were not subjected to exactly the same amount of curtailment in feed (as is set forth in detail in the consideration of the rations on pages 38 and 39), we will examine, first, the results for Group II and subsequently those for Groups III and IV, respectively.

### METABOLISM AS AFFECTED BY A CURTAILMENT IN RATION AMOUNTING TO SOMEWHAT MORE THAN 50 PER CENT OF THE MAINTENANCE REQUIREMENT, GROUP II.

Following a short maintenance period, the steers in Group II, Nos. 1, 3, 7, 10, and 11, were placed upon a ration exclusively of hay, somewhat less than 50 per cent of their supposed maintenance requirements as computed upon the basis of live weight. The low hay ration began with the morning feed of December 22, and continued with but slight modifications through May 5. After this date the animals then received the original maintenance amount of hay for one week, followed in turn by fattening rations. The data for the respiration experiments, including usually 25 to 30 for each animal throughout the year, are presented in a table and chart for each steer, a treatment exactly that accorded the control steers, Nos. 2, 4, and 5.

#### The Course of the Standard Metabolism of Steer 1.

The data for this animal are given in Table 68 and the corresponding chart, Fig. 30. Special consideration has already been given to the first three columns of Table 68 in discussing the method of computing the surface-area (see Table 60, p. 225), and these three columns are reprinted here simply to make for uniformity of tabular treatment of all animals and for the purpose of comparing body-weights and surface-areas. It is unnecessary to consider these values especially, except to point out that while with the control animals the percentage of empty weight to live weight was very constant throughout the maintenance period, with steer 1 the percentages start at 88, decrease with emaciation to 85, and increase again with realimentation until a value of 91 per cent is reached.

The range in temperature during the experiments is not materially different from that noted with the control animals. Indeed, the normal animals serve as a perfect control throughout the entire series. They were in the same barn, were given the same treatment in every detail (with the single exception of receiving a full maintenance ration of hay), and consequently were subjected to the same psychical disturbances, noises, wind, temperature of drinking-water, and every variant other than that of the amount of hay.

The average carbon-dioxide production per half hour, however, has a range with steer 1 that is in no sense comparable to that noted with the 3 control steers. That is, excluding the first experiment on December 7, the maximum carbon-dioxide production per half hour is 89.7 grams and the minimum is 43.8 grams. In other words, the lowest value is essentially one-half of the maximum. It is unfortunate that the maximum value is based upon only one period on January 10, but it is in all probability not far from the true value, for if there had been any obvious defect to explain the high value, it would have been discarded. Entirely aside from this particularly high point, however, the level of the carbon-dioxide production for the first one or two experiments is not far from 75 to 80 grams per half hour, while after the middle of February and until realimentation begins the level is nearer 46 or 47 grams, thus speaking for a tremendous, permanent depression of the metabolism at this low feed-level. With the resumption of full feeding there is a great increase in the carbon-dioxide production. Indeed, the rise from 44.8 grams

on May 5 to 79.6 grams on May 14 seems almost incredible. Had this increase been observed only with this one steer, we might be skeptical as to the accuracy of the tests, but, as will be seen later, a proportionate increase is noted with the other animals subjected to reduced rations and represents a

TABLE 68.—*Body-weight, body-surface, pulse-rate, and standard heat-production per 24 hours, steer 1.*

| Date. | Live weight. | Per cent empty weight ($W$) to live weight. | Body-surface ($0.1186\ W^{.56}$). | No. of periods. | Average temperature of chamber. | Average carbon dioxide produced per half hour. | Heat (computed) per 24 hours.[1] | | | Average pulse-rate per minute. |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | Total. | Per 500 kg. | Per square meter. | |
| 1918–19. | *kg.* | | *sq. m.* | | *°C.* | *gm.* | *cal.* | *cal.* | *cal.* | |
| Dec. 7[2] | [3]581 | 88 | 5.85 | 1 | 6.0 | 74.5 | 11,100 | 9,600 | 1,900 | ..... |
| Jan. 10[4] | 517 | 87 | 5.40 | 1 | 7.0 | 89.7 | 13,300 | 12,900 | 2,460 | 26 |
| Jan. 16 | 507 | 87 | 5.33 | 3 | 10.1 | 77.8 | 11,600 | 11,400 | 2,180 | 26 |
| Jan. 24 | 514 | 87 | 5.38 | 2 | 14.5 | 74.4 | 11,100 | 10,800 | 2,060 | 25 |
| Jan. 30 | 499 | 87 | 5.28 | 2 | 11.0 | 61.3 | 9,100 | 9,100 | 1,720 | 24 |
| Feb. 12 | 501 | 87 | 5.31 | 3 | 9.9 | 51.3 | 7,600 | 7,600 | 1,430 | 24 |
| Feb. 21 | 496 | 87 | 5.26 | 3 | 10.1 | 47.6 | 7,100 | 7,200 | 1,350 | 26 |
| Feb. 27 | 491 | 87 | 5.23 | 4 | 8.4 | 43.8 | 6,500 | 6,600 | 1,240 | 24 |
| Mar. 7 | 484 | 86 | 5.14 | 3 | 12.0 | 48.7 | 7,300 | 7,500 | 1,420 | 25 |
| Mar. 17 | 483 | 86 | 5.13 | 3 | 14.8 | 48.8 | 7,300 | 7,500 | 1,420 | 25 |
| Apr. 8 | 469 | 85 | 5.01 | 3 | 15.8 | 50.9 | 7,600 | 8,100 | 1,520 | 26 |
| Apr. 16 | 454 | 85 | 4.91 | 3 | 14.7 | 44.9 | 6,700 | 7,400 | 1,360 | 26 |
| Apr. 28 | 461 | 85 | 4.95 | 2 | 18.1 | 47.6 | 7,100 | 7,700 | 1,430 | 25 |
| May 5[5] | 454 | 85 | 4.91 | 2 | 18.3 | 44.8 | 6,700 | 7,400 | 1,360 | 25 |
| General av. | ..... | ..... | ..... | ..... | ..... | 56.3 | 8,400 | 8,600 | 1,610 | ..... |
| Av., Feb. 12 to May 5 | ..... | ..... | ..... | ..... | ..... | ..... | ..... | ..... | 1,390 | ..... |
| May 14[6] | 478 | 85 | 5.06 | 3 | 19.7 | 79.6 | 11,100 | 11,600 | 2,190 | ..... |
| May 20 | 505 | 87 | 5.32 | 3 | 23.5 | 70.1 | 9,800 | 9,700 | 1,840 | ..... |
| May 26 | 497 | 87 | 5.26 | 3 | 20.7 | 79.9 | 11,100 | 11,200 | 2,110 | 48 |
| June 3 | 486 | 87 | 5.19 | 3 | 27.9 | 77.9 | 10,800 | 11,100 | 2,080 | 58 |
| June 10 | 499 | 87 | 5.28 | 3 | 17.6 | 81.3 | 11,300 | 11,300 | 2,140 | 59 |
| June 19 | 511 | 87 | 5.36 | 3 | 28.9 | 79.1 | 11,000 | 10,800 | 2,050 | 50 |
| June 24 | 520 | 87 | 5.41 | 3 | 24.9 | 86.1 | 12,000 | 11,500 | 2,220 | 59 |
| June 30 | 542 | 88 | 5.60 | 3 | 21.6 | 85.3 | 11,900 | 11,000 | 2,130 | 59 |
| July 11 | 555 | 88 | 5.68 | 3 | 24.0 | 96.3 | 13,400 | 12,100 | 2,360 | 59 |
| Sept. 6 | 637 | 89 | 6.24 | 3 | 21.8 | 91.2 | 12,700 | 10,000 | 2,040 | 57 |
| Sept. 17 | 653 | 90 | 6.38 | 3 | 21.9 | 102.5 | 14,300 | 10,900 | 2,240 | 61 |
| Oct. 21 | 682 | 91 | 6.60 | 3 | 16.8 | 93.8 | 13,100 | 9,600 | 1,980 | 62 |
| Oct. 29 | 691 | 91 | 6.66 | 3 | 17.8 | 93.6 | 13,000 | 9,400 | 1,950 | 53 |
| General av. | ..... | ..... | ..... | ..... | ..... | 85.9 | 12,000 | 10,800 | 2,100 | ..... |

[1] In Tables 62 to 80, heat computed by assuming 3.1 calories per gram $CO_2$ for all dates through May 12, and 2.9 calories for all dates after May 12, unless stated otherwise.

[2] Steer had 10.4 kg. hay, Dec. 5, and 5.2 kg., Dec. 6; received only half daily ration, Dec. 6, evening feed being withheld because of respiration experiment Dec. 7; half ration not received on Dec. 6 made up on Dec. 8 as midday meal.

[3] Weight on Dec. 9; not weighed on Dec. 7.

[4] Steer had 4.5 kg. hay, Jan. 8, and 2.3 kg., Jan. 9; received only half daily ration Jan. 9, evening feed being withheld because of respiration experiment on Jan. 10; half ration not received on Jan. 9 made up on Jan. 11 as midday meal.

[5] Steer had 4.5 kg. hay per day on May 1 to 3, inclusive, and 2.2 kg. on May 4.

[6] Steer had 12.2 kg. hay, May 12, and 5.0 kg. hay and 2.3 kg. grain, May 13.

physiological fact. The highest carbon-dioxide production of steer 1 is 102.5 grams on September 17, during the period of heavy feeding.

The carbon-dioxide production per half hour, although it is the factor that was actually measured in the experiments, is not suitable for such general

application and interpretation, however, as is the heat-production computed from the carbon-dioxide production and expressed on the three bases of the total amount produced per 24 hours, the amount produced per 500 kg. of body-weight per 24 hours and, finally, that produced per square meter of body-surface per 24 hours. Considering, first, the total heat-production, we find that steer 1 at the beginning had a standard metabolism of not far from 12,000 calories. After a few weeks of curtailed ration a low level of not far from 7,000 calories was reached, and this low level remained constant until realimentation began. The change in the total heat-production from 12,000 calories to about 7,000 calories represents a decrease of approximately 40 per cent. Expressed in other terms, steer 1 had a standard metabolism or an energy need after the middle of February amounting to but 60 per cent of that obtaining during December and January. With the resumption of full feed the total caloric output increased greatly, reaching practically the initial level. As the weight increases toward the end of the fattening period, there is a distinct tendency for the values to rise even somewhat higher, on the average to not far from 13,300 calories per 24 hours. If minimum and maximum values are compared, it can be seen that on February 27, April 16, and May 5 (the last day of submaintenance) this animal had a minimum standard heat-production of 6,500, 6,700, and 6,700 calories, respectively, and on September 17 a maximum heat-production of 14,300 calories, or more than twice as great.

Since steer 1 underwent great weight changes, it is important to consider the values when referred to equal weight, such as the 500-kg. basis. By this method of computation we find that at the start the heat-production per 500 kg. per 24 hours is not far from 10,000 to 11,000 calories. During the period of low maintenance, however, even on the basis of equal weight there is a striking decrease in metabolism and the tendency is for the heat-production to be not far from 7,500 calories. With realimentation the heat-production per 500 kg. returns to the high level, but on the last two dates falls off to 9,600 and 9,400 calories, respectively. This latter fact suggests that possibly the increase in weight which has taken place, since it is in part inert fat, does not enter into the metabolism, and therefore dilutes, so to speak, the metabolism per unit of weight, although the evidence of Armsby suggests that the deposition of fat actually stimulates metabolism.

From the physiological standpoint it is of importance, particularly under conditions of great weight changes such as these animals experienced, to attempt to secure the closest possible measurement of the standard metabolism, and many writers consider the computation of the heat-production per square meter of body-surface as the best index. These computations on the basis of surface-area (obtained by use of the Moulton constants) are recorded for steer 1 in the next to the last column of Table 68. On this basis the metabolic level at the beginning of the experiment is not far from 2,000 calories, but there is a great decrease during the submaintenance period to a level nearer 1,400 calories. In other words, even on the basis of equal surface-area, steer 1, during the submaintenance period, had a standard metabolism approximately but two-thirds that when on full feed. With refeeding the heat-production per square meter of body-surface returns to the original level and

remains rather remarkably constant throughout the rest of the experimental year at not far from 2,100 calories.

From the comparison of the results shown in Table 68, two rather distinct phases of this study of metabolism suggest themselves. In the first place, steer 1, while on the curtailed ration, is subsisting with a very much lower demand for energy per 24 hours. This is irrespective of whether or no the energy of the feed suffices for maintenance. Even when referred to the unit of body-weight the demand for energy is very greatly altered, which would indicate that the reference to the unit of weight does not eliminate this inequality in metabolic activity, and even when the supposedly unifying method of reference to equal surface-area is employed, the metabolism is still very low during the period of submaintenance. In other words, the picture is clear that there is a marked lowering of the metabolism, not only for the individual as a

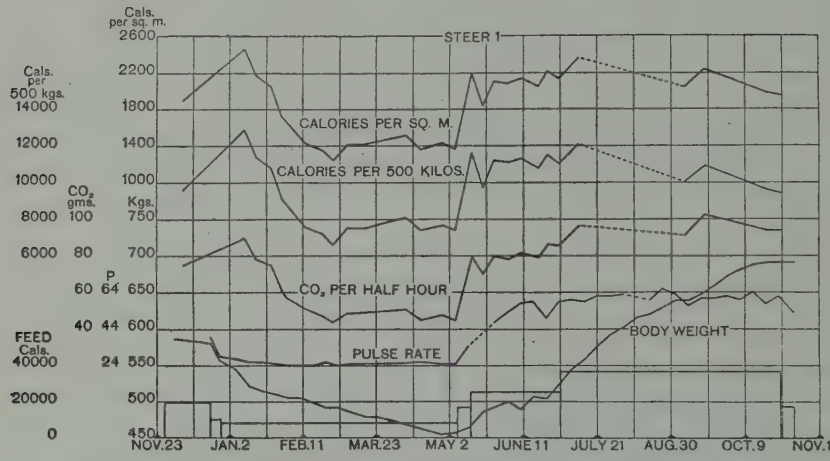


FIG. 30.—Curves for body-weight, pulse-rate per minute, carbon-dioxide production per half hour, and heat-production per 500 kg. of body-weight per 24 hours and per square meter of body-surface per 24 hours, and blocks for metabolizable energy in feed per day, steer 1.

whole, but per unit of weight and per unit of surface-area, and that the animal is living on a lower nutritive plane with a very greatly diminished metabolic activity. In the second place, with the resumption of full feeding the metabolism immediately rises to an entirely different plane, but the rise is by no means commensurate with the increase in body-weight. Thus, with the change from the submaintenance quantity of hay to the full-maintenance allowance of hay for one week, the total metabolism increased from 6,700 calories to 11,100 calories per 24 hours, with proportionate increases on the other two bases of computation.

For the purpose of visualizing better these great changes in metabolism, all of the results have been recorded graphically in Fig. 30.[a] From this chart it

[a] As already stated (see p. 228), the curves for body-weight and pulse-rate in this and the following charts were plotted from 7-day averages and not from daily records. The curves for carbon-dioxide and heat-production were plotted from the data given in the detailed Tables 62 to 80 for the different steers, and the blocks representing metabolizable energy in feed were based on average values given in Tables 41 to 44, inclusive.

can be seen that the curves for the carbon-dioxide production per half hour and for the heat-production computed therefrom, both per 500 kg. of body-weight and per square meter of body-surface per 24 hours, fall off pronouncedly during the first part of the submaintenance period until about the first of March. Thereafter they remain at practically a constant level until realimentation begins, when there is at once a marked rise in all the curves, followed by a slight though steady rise to the end of the experiment as the fattening process continues. These metabolism curves do not directly parallel the body-weight curve, which falls off steadily from the beginning of the submaintenance period to the beginning of the realimentation period, while the metabolism curves fall rapidly for the first 2 months and thereafter remain relatively constant. During realimentation, both the metabolism and the weight curves rise. As a matter of fact, the metabolism increases more markedly at first than the weight. The pulse-rate has already been discussed (see p. 184).

To indicate the relationship between the physiological functions and the ration, blocks are drawn at the bottom of Figs. 30 to 34 showing the total metabolizable energy in the feed given, and they are so drawn as to show the approximate average amounts in periods when material changes in feed were made. Of special importance is, first, the so-called "maintenance" period, then the long submaintenance period, and finally, the successive steps of the realimentation period. As already pointed out, the basis of computation for the first or maintenance amount of feed was the live body-weight, and when it is stated that with Group II the feed was cut somewhat more than 50 per cent, it means somewhat more than 50 per cent of the initial ration. Since there are considerable decreases in body-weight, it is obvious that at the end of the submaintenance period the animals were receiving a ration somewhat more than 50 per cent of maintenance, computed upon the then existing body-weight. It must again be emphasized that the quantities indicated on the charts are only approximately correct and represent very general averages. (See Table 43, p. 170.) Reference to the detailed feed table (see Table 3, p. 38) must be made for the individual daily amounts of feed received. As a help, particularly in interpreting the noticeable increase in metabolism following the increase in feed in May, the footnotes to Table 68 and the other tables in this series are so arranged as to give individual amounts of feed (as eaten, not as water-free substance) for a day or two before the first day of each important change in ration.

It is particularly unfortunate that with all our steers subjected to curtailed rations we obtained but one metabolism measurement during the maintenance period, that is, about the first week in December. The rations were cut December 22. It is apparent in the particular case of steer 1, at least, that the metabolism had not been affected by the change in ration 2½ weeks later, namely, January 10. Indeed, as late as January 24 his metabolism is as high as that noted in the normal maintenance period, and it is some time after the curtailment in ration before the low level of metabolic activity is indicated. This has an important bearing upon the interpretation of the great increase in metabolism following realimentation, for since our method of computing the heat-production is based entirely upon the carbon-dioxide production, one might argue that the high values found with steer 1 and other animals at the beginning of realimentation were due to a more or less delayed

digestive activity or fermentative action in the intestinal tract, caused by the increased fill. It should be pointed out, however, that on January 10 steer 1 had already been upon a ration somewhat less than one-half maintenance for 2½ weeks, during which time the fill unquestionably had decreased materially, and the values found on January 10 and in the subsequent 2 weeks are simply an expression of the previous high metabolic plane, which reacts to undernutrition only slowly. On the other hand, with realimentation there is an immediate stimulus to metabolism, due to the increased supply of food material.

There is a steady decrease in the metabolic activity during the first four experiments of the submaintenance period, and a constant level is not reached until about February 12. Average values for the entire submaintenance period show that the carbon-dioxide production per half hour is 56.3 grams, the total heat-production is 8,400 calories, the heat-production per 500 kg. of body-weight is 8,600 calories, and that per square meter of body-surface 1,610 calories. These averages do not, however, represent the low level of approximately 3 months from the first of February to the first of May, for they include the distinctly high values for the first four experiments, when the metabolism was adjusting itself slowly to the lower level. Excluding these first four values, the averages for the low level from February 12 to May 5, inclusive, are as follows: carbon-dioxide production per half hour, 47.6 grams; total heat-production per 24 hours, 7,100 calories; heat-production per 500 kg. of body-weight per 24 hours, 7,400 calories; heat-production per square meter of body-surface per 24 hours, 1,390 calories. During the realimentation period there is a great increase in the carbon-dioxide and computed heat-production. While there is a slight tendency for the total heat-production to increase with the continuation of the fattening period, the heat-production per 500 kg. of body-weight and per square meter of body-surface throughout the entire period are reasonably expressed by the average values of 10,800 and 2,100 calories, respectively. If we compare the average values for the fattening period with those obtained at the low level of submaintenance from February 12 to May 5, we find an average increase of 38.3 grams in the carbon-dioxide production, of 4,900 calories in the total heat-production, of 3,400 calories in the heat-production per 500 kg. of body-weight, and of 710 calories in the heat-production per square meter of body-surface, increases of a very great order. If, as we believe, the computation of the heat-production from the carbon-dioxide production represents the true heat-production, unaffected (to any considerable extent at least) by digestive activity, the differences noted in the average heat-values indicate clearly that steer 1 was living on two very widely differing nutritive planes.

Comparison of these findings with those in the case of the control steers is perfectly justifiable and can well be made. Since we have so much other information with regard to the influence of low rations, however, it seems best to defer any comparison with the control steers until the other members of this submaintenance group (Group II) are considered more in detail.

### The Course of the Standard Metabolism of Steer 3.

The detailed data for the whole series of experiments on steer 3, the second animal in Group II, are shown in Table 69 and in the accompanying chart,

Fig. 31. The essential points noted with steer 1 also appear here, such as changes in the percentage of empty weight, depending upon the degree of emaciation or of fatness, the variability in the temperature of the apparatus (with extremes not unlike those noted with the other animals), and especially

TABLE 69.—*Body-weight, body-surface, pulse-rate, and standard heat-production per 24 hours, steer 3.*

| Date. | Live weight. | Per cent empty weight (W) to live weight. | Body-surface ($0.1186\ W^{2/3}$). | No. of periods. | Average temperature of chamber. | Average carbon dioxide produced per half hour. | Heat (computed) per 24 hours. | | | Average pulse-rate per minute. |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | Total. | Per 500 kg. | Per square meter. | |
| 1918–19. | *kg.* | | *sq. m.* | | *°C.* | *gm.* | *cal.* | *cal.* | *cal.* | |
| Dec. 3[1] | [2]505 | 89 | 5.39 | 4 | ..... | 82.1 | 12,200 | 12,100 | 2,260 | ..... |
| Jan. 10[3] | 446 | 88 | 4.95 | 2 | 8.6 | 77.6 | 11,500 | 12,900 | 2,320 | 31 |
| Jan. 16 | 437 | 88 | 4.90 | 3 | 11.7 | 65.1 | 9,700 | 11,100 | 1,980 | 29 |
| Jan. 25 | 436 | 88 | 4.89 | 3 | 10.5 | 61.6 | 9,200 | 10,600 | 1,880 | 30 |
| Jan. 30 | 432 | 88 | 4.86 | 3 | 12.7 | 59.5 | 8,900 | 10,300 | 1,830 | 30 |
| Feb. 6 | 430 | 88 | 4.84 | 4 | 10.2 | 47.7 | 7,100 | 8,300 | 1,470 | 29 |
| Feb. 17 | 422 | 88 | 4.79 | 3 | 8.0 | 50.2 | 7,500 | 8,900 | 1,570 | 28 |
| Feb. 25 | 415 | 87 | 4.70 | 3 | 10.6 | 41.9 | 6,200 | 7,500 | 1,320 | 28 |
| Mar. 4 | 413 | 87 | 4.69 | 3 | 13.5 | 46.9 | 7,000 | 8,500 | 1,490 | 30 |
| Mar. 17 | 403 | 86 | 4.59 | 3 | 14.2 | 45.4 | 6,800 | 8,400 | 1,480 | 30 |
| Apr. 9 | 398 | 86 | 4.55 | 3 | 15.1 | 51.4 | 7,600 | 9,500 | 1,670 | 33 |
| Apr. 17 | 386 | 86 | 4.46 | 3 | 15.1 | 50.0 | 7,400 | 9,600 | 1,660 | 33 |
| Apr. 23 | 385 | 86 | 4.46 | 3 | 18.2 | 47.9 | 7,100 | 9,200 | 1,590 | 32 |
| May 1[4] | 387 | 86 | 4.47 | 3 | 18.3 | 44.5 | 6,600 | 8,500 | 1,480 | 31 |
| General av. | ..... | ..... | ..... | ..... | ..... | 53.1 | 7,900 | 9,500 | 1,670 | ..... |
| Av., Feb. 6 to May 1 | ..... | ..... | ..... | ..... | ..... | ..... | ..... | ..... | 1,530 | ..... |
| May 10[5] | 411 | 87 | 4.68 | 3 | 17.5 | 67.8 | 10,100 | 12,300 | 2,160 | ..... |
| May 20[6] | 425 | 88 | 4.81 | 3 | 22.2 | 66.9 | 9,300 | 10,900 | 1,930 | 51 |
| May 26 | 420 | 88 | 4.78 | 3 | 21.7 | 69.5 | 9,700 | 11,500 | 2,030 | 51 |
| June 4 | 420 | 88 | 4.78 | 3 | 27.0 | 70.7 | 9,800 | 11,700 | 2,050 | ..... |
| June 10 | 440 | 88 | 4.91 | 3 | 19.6 | 83.9 | 11,700 | 13,300 | 2,380 | 77 |
| June 20 | 448 | 88 | 4.97 | 3 | 28.1 | 81.0 | 11,300 | 12,600 | 2,270 | 64 |
| June 24 | 467 | 89 | 5.14 | 3 | 28.0 | 89.7 | 12,500 | 13,400 | 2,430 | 71 |
| July 1 | 489 | 89 | 5.29 | 1 | 26.2 | 77.9 | 10,800 | 11,000 | 2,040 | 73 |
| July 11 | 480 | 89 | 5.22 | 3 | 25.3 | 88.1 | 12,300 | 12,800 | 2,360 | 65 |
| Sept. 6 | 549 | 90 | 5.72 | 3 | 24.7 | 101.1 | 14,100 | 12,800 | 2,470 | 67 |
| Sept. 12 | 563 | 90 | 5.82 | 3 | 23.3 | 93.9 | 13,100 | 11,600 | 2,250 | 68 |
| Oct. 16 | 603 | 91 | 6.11 | 3 | 18.5 | 90.1 | 12,500 | 10,400 | 2,050 | 73 |
| Oct. 21 | 595 | 91 | 6.06 | 3 | 18.4 | 95.3 | 13,300 | 11,200 | 2,190 | ..... |
| Oct. 29 | 615 | 91 | 6.19 | 3 | 17.9 | 77.9 | 10,800 | 8,800 | 1,740 | ..... |
| General av. | ..... | ..... | ..... | ..... | ..... | 82.4 | 11,500 | 11,700 | 2,170 | ..... |

[1] Steer had 11.4 kg. hay Dec. 1 and 9.8 kg. hay Dec. 2. On Dec. 2 had evening feed, but was not studied in respiration chamber Dec. 3 until 8 p. m.; hence fasting 24 hours before experiment of Dec. 3, as on all other dates.

[2] Weight on Dec. 2; not weighed on Dec. 3.

[3] Steer had 4.1 kg. hay Jan. 8 and 2.0 kg. hay Jan. 9.

[4] From Apr. 28 to May 5, inclusive, steer had 4.1 kg. hay per day, except that on April 30 evening feed withheld because of respiration experiment on May 1.

[5] Steer had 8.2 kg. hay May 6; 8.1 kg. May 7; 9.0 kg. May 8; and 5.2 kg. May 9.

[6] Steer had 10.8 kg. hay and 3.2 kg. grain May 18; on May 19 no hay given, but steer finishing eating hay not eaten on May 18, and also had 3.2 kg. grain.

the wide range in the carbon-dioxide production between the normal period in December and the submaintenance period after the low level of metabolic intensity had been reached. With steer 3 the carbon-dioxide production is about 80 grams per half hour, on the average, for the month of December and the first part of January, and reaches a minimum of 41.9 grams on Feb-

ruary 25. The level throughout the months of February, March, and April, however, is not far from 47 grams per half hour on the average. With the resumption of the full hay ration, when the amount of feed is brought back to the amount given on December 3, there is a great increase in the carbon-dioxide production on May 10, which steadily continues throughout the fattening period, with a maximum of 101.1 grams on September 6.

Giving particular attention, however, to the total heat-production as computed from the carbon-dioxide production, we find the level at the beginning of the experiment is not far from 12,000 calories. As the submaintenance period continues, the total heat-production falls off rapidly to a general level of not far from 7,000 calories, at which level it remains essentially constant during the 3 months from February 6 to May 1. With realimentation a great increase takes place in 9 days, i. e., from 6,600 calories on May 1 (when steer 3 was receiving a submaintenance ration) to 10,100 calories on May 10 (when he was on a full hay ration). As steer 3 is fattened, the total standard metabolism has a tendency to increase throughout the rest of the season. With regard to the heat-production per 500 kg. of body-weight per 24 hours, the initial base-line is also not far from 12,000 calories. At the minimum point the level is approximately 8,700 calories, but with refeeding the original base-line of 12,000 calories is quickly reached, with considerable variations about this level. An especially noticeable result is that obtained on the last day, October 29, when the heat-production per 500 kg. of body-weight is but 8,800 calories, a level not far from that found during the lowest period of submaintenance. Since, however, steer 3 has in the meantime gained over 200 kg., it is probable that here again we have evidence of an addition of considerable inert fat without this playing a great rôle in the metabolism. Against this hypothesis, on the other hand, is the fact that but 8 days before, on October 21, steer 3 had a 24-hour heat-production amounting to 11,200 calories per 500 kg. of body-weight. Both experiments are based upon three periods and we have no explanation for this wide difference. On the basis of the heat-production per square meter of body-surface, the initial level is not far from 2,300 calories, falling during the submaintenance period to not far from 1,500 calories, from which point the initial level is resumed and, indeed, exceeded with refeeding. The very low value of 1,740 calories per square meter of body-surface on October 29 is comparable to the low value noted on the basis of the calculation per 500 kg. of body-weight and is not easily explained.

In Fig. 31 the general trend of the curves is quite similar to that observed with steer 1, and although direct comparison between the two steers is not easily made, a method of comparison will be subsequently given. The curves for body-weight, carbon-dioxide production, and heat-production all fall off, but while the body-weight decreases regularly throughout the entire period of submaintenance, the carbon-dioxide production and heat-production fall rapidly at first, reach a seemingly constant level about the first of February and remain at this level throughout the period of submaintenance feeding, with fluctuations above and below the general average line. The tremendous increases upon refeeding are characteristic and precede the great rise in body-weight.

Throughout the entire submaintenance period from January 10 to May 1, inclusive, the average carbon-dioxide production per half hour is 53.1 grams, the total 24-hour heat-production 7,900 calories, the 24-hour heat-production per 500 kg. of body-weight 9,500 calories, and that per square meter of body-surface 1,670 calories, but these averages include the high results during the first four experiments, exactly as in the case of steer 1. Excluding these first four values, which represent more or less a period of adjustment to the lower nutritive plane, we find that for the 3 months, February, March, and April, the average carbon-dioxide production per half hour is 47.3 grams, the average total 24-hour heat-production is 7,000 calories, that per 500 kg. of body-weight is 8,700 calories, and that per square meter of body-surface is 1,530 calories. Compared with this last series of figures are the average values for the realimentation period, which are 82.4 grams of carbon-dioxide, 11,500 calories per 24 hours, 11,700 calories per 500 kg. of body-weight per 24 hours, and 2,170 calories per square meter of body-surface per 24 hours. This comparison accentuates the tremendous difference in the nutritive planes on which steer 3 was living at the two different periods of the experiment.

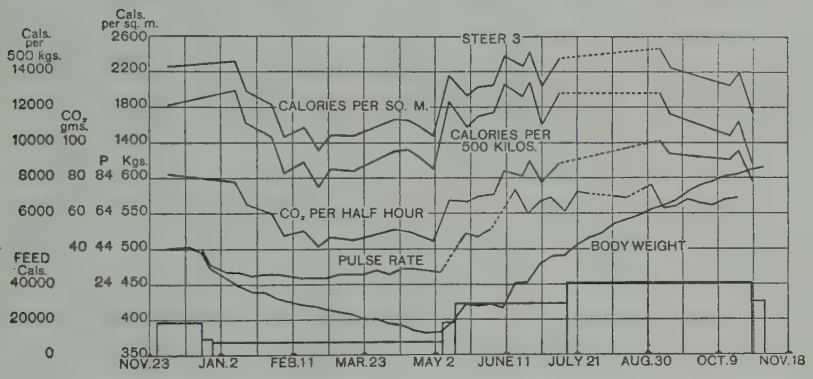


FIG. 31.—Curves for body-weight, pulse-rate per minute, carbon-dioxide production per half hour, and heat-production per 500 kg. of body-weight per 24 hours and per square meter of body-surface per 24 hours, and blocks for metabolizable energy in feed per day, steer 3.

### THE COURSE OF THE STANDARD METABOLISM OF STEER 7.

The third animal in this series, steer 7, was somewhat smaller than the other steers in Group II and also the youngest. The detailed results for steer 7 are given in Table 70 and the accompanying chart, Fig. 32. As a result of the curtailment in ration, there was a great lowering in body-weight, accompanied by changes in the estimated percentages of empty weight and in the surface-area. In the entire series of experiments there were no days on which less than two periods were used for estimating the average values, indeed, almost invariably three periods were used, and on December 6, the very first day, five periods. The range in temperature was essentially that noted in the experiments with the other steers, a minimum of 7.5° C. appearing on February 20 with a maximum of 29.1° C. on September 8. The carbon-dioxide production per half hour has the usual variations noted with

these animals on low rations, the maximum being 69.5 grams and the minimum being 39.9 grams, a decrease approximately proportional to that noted with the other animals of Group II.

The total 24-hour heat-production drops after a few weeks from an initial normal level of 10,300 calories to a submaintenance level of about 6,200 calories, with a striking increase on May 12 coincidental with the increased

TABLE 70.—*Body-weight, body-surface, pulse-rate, and standard heat-production per 24 hours, steer 7.*

| Date. | Live weight. | Per cent empty weight ($W$) to live weight. | Body-surface ($0.1186\ W^{2/3}$). | No. of periods. | Average temperature of chamber. | Average carbon dioxide produced per half hour. | Heat (computed) per 24 hours. | | | Average pulse-rate per minute. |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | Total. | Per 500 kg. | Per square meter. | |
| 1918–19. | *kg.* | | *sq. m.* | | °*C.* | *gm.* | *cal.* | *cal.* | *cal.* | |
| Dec. 6[1] | [2]467 | 89 | 5.14 | 5 | ..... | 69.5 | 10,300 | 11,000 | 2,000 | ..... |
| Jan. 11[3] | 406 | 88 | 4.67 | 2 | 12.4 | 63.6 | 9,500 | 11,700 | 2,030 | 40 |
| Jan. 23 | 395 | 88 | 4.60 | 3 | 16.3 | 66.3 | 9,900 | 12,500 | 2,150 | 36 |
| Feb. 4 | 393 | 88 | 4.58 | 3 | 11.8 | 52.6 | 7,800 | 9,900 | 1,700 | 35 |
| Feb. 13 | 374 | 87 | 4.41 | 3 | 9.2 | 49.5 | 7,400 | 9,900 | 1,680 | 32 |
| Feb. 20 | 371 | 87 | 4.39 | 3 | 7.5 | 45.5 | 6,800 | 9,200 | 1,550 | 32 |
| Mar. 3 | 377 | 87 | 4.43 | 3 | 14.2 | 51.7 | 7,700 | 10,200 | 1,740 | 30 |
| Mar. 11 | 371 | 87 | 4.39 | 3 | 14.6 | 41.4 | 6,200 | 8,400 | 1,410 | 30 |
| Apr. 10 | 355 | 86 | 4.23 | 3 | 14.4 | 41.6 | 6,200 | 8,700 | 1,470 | 31 |
| Apr. 19 | 352 | 86 | 4.22 | 3 | 15.7 | 42.6 | 6,300 | 8,900 | 1,490 | 30 |
| Apr. 24[4] | 352 | 86 | 4.22 | 3 | 16.0 | 43.5 | 6,500 | 9,200 | 1,540 | 33 |
| Apr. 29[4] | 352 | 86 | 4.22 | 3 | 16.5 | 39.9 | 5,900 | 8,400 | 1,400 | 29 |
| General av. | ..... | ..... | ..... | ..... | ..... | 48.9 | 7,300 | 9,700 | 1,650 | ..... |
| Av., Mar. 11 to Apr. 29. | ..... | ..... | ..... | ..... | ..... | ..... | ..... | ..... | 1,460 | ..... |
| May 12[5] | 389 | 88 | 4.55 | 3 | 18.0 | 60.4 | 9,000 | 11,600 | 1,980 | 38 |
| May 22 | 390 | 88 | 4.56 | 3 | 19.7 | 65.7 | 9,100 | 11,700 | 2,000 | 55 |
| May 28 | 385 | 88 | 4.52 | 3 | 22.1 | 60.4 | 8,400 | 10,900 | 1,860 | 62 |
| June 6 | 392 | 88 | 4.57 | 3 | 25.7 | 65.4 | 9,100 | 11,600 | 1,990 | 61 |
| June 20 | 422 | 88 | 4.79 | 3 | 25.4 | 72.5 | 10,100 | 12,000 | 2,110 | 60 |
| June 27 | 426 | 88 | 4.82 | 3 | 26.8 | 82.9 | 11,500 | 13,500 | 2,390 | 66 |
| July 7 | 436 | 89 | 4.92 | 3 | 28.7 | 72.2 | 10,100 | 11,600 | 2,050 | 63 |
| Sept. 8 | 522 | 90 | 5.55 | 3 | 29.1 | 97.8 | 13,600 | 13,000 | 2,450 | 70 |
| Sept. 12 | 539 | 90 | 5.66 | 3 | 22.8 | 86.8 | 12,100 | 11,200 | 2,140 | 65 |
| Oct. 20 | 591 | 91 | 6.04 | 3 | 17.8 | 93.9 | 13,100 | 11,100 | 2,170 | 65 |
| Oct. 27 | 592 | 91 | 6.04 | 3 | 20.8 | 91.9 | 12,800 | 10,800 | 2,120 | 65 |
| General av. | ..... | ..... | ..... | ..... | ..... | 77.3 | 10,800 | 11,700 | 2,110 | ..... |

[1] Steer had 7.4 kg. hay Dec. 4; 4.0 kg. Dec. 5.
[2] Weight on Dec. 9; not weighed on Dec. 6.
[3] Steer had 3.6 kg. hay Jan. 9; 1.8 kg. Jan. 10.
[4] Steer had 3.6 kg. hay Apr. 21 to May 5, inclusive, except when evening feed withheld because of respiration experiment.
[5] Steer had 7.2 kg. hay May 6 and 7; 8.8 kg. May 8; 8.0 kg. May 9; 7.5 kg. May 10; no hay given May 11, but steer finished eating hay given May 10.

hay ration. Thereafter the total heat-production tends to rise gradually with the increasing weight of the steer, until the end of the experiment, when a level of about 13,000 calories is obtained on full feed of hay and grain. Owing to the wide variations in body-weight and the fact that steer 7 was a somewhat smaller animal than the other steers in Group II, the calculations per 500 kg. of body-weight are specially significant. On this basis the heat-production has an initial level of 11,000 calories, which changes to about 8,700 calories during the last 2 months of the submaintenance period and returns to

about 11,000 calories or more with realimentation. Finally, the heat-production per square meter of body-surface begins at a level of about 2,000 calories, and during the period of submaintenance drops to a level of not far from 1,500 calories, returning to 2,000 calories and even higher toward the end of the realimentation period, the last seven values averaging clearly somewhat above 2,200 calories. The general picture is exactly that exhibited by steers 1 and 3, namely, a great depression of the metabolism accompanying the curtailment in ration, an immediate, almost explosive increase in metabolism following the resumption of the full maintenance quantity of hay, and a further steady increase in the total metabolic activity as the steer changes in weight and goes onto a distinctly higher nutritive plane.

As evidence contributing toward the fact that these increases in the carbon-dioxide production are true measures of metabolic intensity and not contaminated by the influence either of the immediate or the after effect of the feed ingested, such as digestion including fermentative changes, the experimental results obtained on May 12 with steer 7 are of special importance, for on the day before, May 11 (as can be seen from footnote 5 in Table 70), this animal received no hay, but finished eating the hay given on May 10. In general, the steers were fed on the morning of the day before a respiration experiment, but received no feed during the rest of the day, so that on the following day the respiration experiment was made 24 hours after the last feed was given. In this particular case steer 7 received 7.5 kg. of hay on May 10, of which 5 kg. were given at $4^h\ 30^m$ p. m. No further feed was given thereafter until after the respiration experiment on May 12. In spite of this longer period after feed ingestion, there was a great increase in the carbon-dioxide production from 39.9 grams on April 29 to 60.4 grams on May 12. During this time there was an increase of 37 kg. in the body-weight, in large part undoubtedly as a result of increased fill. We believe that these figures speak for a definite increase in the metabolism due to the higher ration, uncontaminated to any appreciable extent, at least, by carbon dioxide resulting from the processes of digestion.

Considering the entire submaintenance period and averaging all the results obtained therein, we find an average production of 48.9 grams of carbon dioxide per half hour, 7,300 calories per 24 hours, 9,700 calories per 500 kg. of body-weight per 24 hours, and 1,650 calories per square meter of body-surface per 24 hours. With steer 7, apparently the period of adjustment to the low ration was somewhat longer than with steers 1 and 3, for it is not until March 11, about 2½ months after the beginning of the curtailed ration, that we find the low level of metabolism. From March 11 to April 29 this level remains essentially constant, the average values being 41.8 grams of carbon dioxide per half hour, 6,200 calories per 24 hours, 8,700 calories per 500 kg. of body-weight per 24 hours, and 1,460 calories per square meter of body-surface per 24 hours. Averaging all the data for the realimentation period, we find 77.3 grams of carbon dioxide produced per half hour, 10,800 calories per 24 hours, 11,700 calories per 500 kg. of body-weight per 24 hours, and 2,110 calories per square meter of body-surface per 24 hours.

At this point emphasis should be laid upon the fact that in any comparison between the two nutritive planes during submaintenance feeding and realimentation, the *last* part of the realimentation period, when higher values

than the average are found, should, strictly speaking, be considered. But even if we simply compare the average values for the entire realimentation period with the low level from March 11 to April 29, inclusive, the great difference in the nutritive planes is at once made clear, a difference fully in accord with the differences noted with steers 1 and 3.

The presentation of the data in Fig. 32 for steer 7 requires no special comment, as the picture is essentially that presented in the charts for steers 1 and 3.

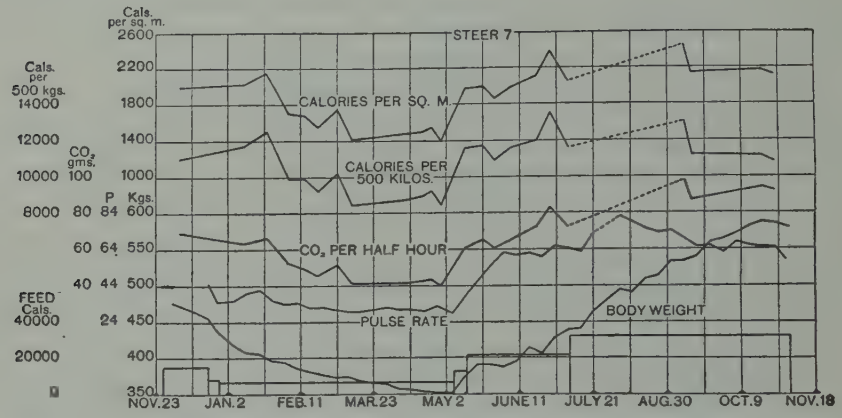


FIG. 32.—Curves for body-weight, pulse-rate per minute, carbon-dioxide production per half hour, and heat-production per 500 kg. of body-weight per 24 hours and per square meter of body-surface per 24 hours, and blocks for metabolizable energy in feed per day, steer 7.

### THE COURSE OF THE STANDARD METABOLISM OF STEER 10.

The data for the several experiments with the fourth animal in Group II, steer 10, are recorded in Table 71 and the corresponding chart, Fig. 33. Steer 10 was subjected to exactly the same curtailment of ration, namely, somewhat more than 50 per cent of the maintenance requirement, and with this steer the loss in body-weight and the changes in the percentage of empty weight to live weight and in the computed surface-areas all follow essentially the same course noted with the other steers of this group. The range in temperature is also much the same. The carbon-dioxide production per half hour has a high initial value of 97.7 grams, followed by a great decrease until toward the end of the submaintenance period, when a minimum of 41.5 grams is observed, or less than one-half that at the start. Indeed, the level during the last two-thirds of the submaintenance period is not far from 50 grams, or practically one-half that of the initial value.

In considering the metabolism during the realimentation period, it must be recalled that in this period steer 10 received somewhat different treatment from the other steers in Group II. Thus, while the other animals in this group received during the first week (May 6 to 12) after the submaintenance period double the amount of metabolizable energy in hay that they had been receiving during the submaintenance period, and after May 12 heavy rations of both hay and grain, this was not the case with steer 10. In the realimentation of steer 10, the attempt was made to give him at first sufficient metabo-

lizable energy in the form of hay alone to furnish a maintenance ration, based on his original initial body-weight, the idea being to have him regain his lost weight on hay only. This maintenance ration of hay was given until July 8, on and after which date both hay and grain were given. Owing to the disturb-

TABLE 71.—*Body-weight, body-surface, pulse-rate, and standard heat-production per 24 hours, steer 10.*

| Date. | Live weight. | Per cent empty weight ($W$) to live weight. | Body-surface ($0.1186\ W^{.56}$). | No. of periods. | Average temperature of chamber. | Average carbon dioxide produced per half hour. | Heat (computed)[1] per 24 hours. | | | Average pulse-rate per minute. |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | Total. | Per 500 kg. | Per square meter. | |
| 1918–19. | *kg.* | | *sq. m.* | | *°C.* | *gm.* | *cal.* | *cal.* | *cal.* | |
| Dec. 5[2] | [3]594 | 89 | 5.97 | 3 | ..... | 97.7 | 14,500 | 12,200 | 2,430 | ..... |
| Jan. 11[4] | 522 | 88 | 5.47 | 5 | 6.9 | 67.9 | 10,100 | 9,700 | 1,850 | 36 |
| Jan. 20 | 513 | 88 | 5.41 | 3 | 10.6 | 60.4 | 9,000 | 8,800 | 1,660 | 30 |
| Feb. 3 | 494 | 87 | 5.25 | 2 | 11.9 | 56.5 | 8,400 | 8,500 | 1,600 | 31 |
| Feb. 13 | 492 | 87 | 5.23 | 3 | 12.6 | 46.0 | 6,800 | 6,900 | 1,300 | 32 |
| Feb. 24 | 489 | 87 | 5.21 | 3 | 12.4 | 47.7 | 7,100 | 7,300 | 1,360 | 32 |
| Mar. 6 | 487 | 87 | 5.21 | 3 | 13.3 | 52.0 | 7,700 | 7,900 | 1,480 | 36 |
| Mar. 18 | 473 | 87 | 5.11 | 2 | 15.1 | 52.4 | 7,800 | 8,200 | 1,530 | 35 |
| Apr. 14 | 460 | 86 | 4.98 | 3 | 17.8 | 52.7 | 7,800 | 8,500 | 1,570 | 33 |
| Apr. 22 | 459 | 86 | 4.98 | 3 | 15.0 | 53.3 | 7,900 | 8,600 | 1,590 | 34 |
| Apr. 29 | 454 | 86 | 4.94 | 3 | 17.0 | 41.5 | 6,200 | 6,800 | 1,260 | 37 |
| May 3 | 457 | 86 | 4.96 | 3 | 17.6 | 49.3 | 7,300 | 8,000 | 1,470 | 37 |
| May 8[5] | 454 | 86 | 4.94 | 3 | 18.0 | 48.9 | 7,300 | 8,000 | 1,480 | 42 |
| General av. | ..... | ..... | ..... | ..... | ..... | 52.4 | 7,800 | 8,100 | 1,510 | ..... |
| Av., Feb. 13 to May 8 | ..... | ..... | ..... | ..... | ..... | ..... | ..... | ..... | 1,450 | ..... |
| May 16[6] | 489 | 87 | 5.21 | 3 | 17.8 | 57.2 | 8,500 | 8,700 | 1,630 | 47 |
| May 23[7] | 494 | 87 | 5.25 | 3 | 20.3 | 57.5 | 8,600 | 8,700 | 1,640 | 46 |
| June 2 | 494 | 87 | 5.25 | 3 | 25.7 | 58.2 | 8,700 | 8,800 | 1,660 | 42 |
| June 7 | 496 | 87 | 5.26 | 3 | 28.2 | 63.5 | 9,400 | 9,500 | 1,790 | 49 |
| June 19 | 487 | 87 | 5.21 | 3 | 20.3 | 57.0 | 8,500 | 8,700 | 1,630 | 51 |
| June 23 | 464 | 87 | 5.05 | 3 | 16.5 | 45.6 | 6,800 | 7,300 | 1,350 | 51 |
| June 28 | 495 | 87 | 5.25 | 3 | 20.7 | 60.4 | 9,000 | 9,100 | 1,710 | 48 |
| July 9[8] | 490 | 87 | 5.22 | 3 | 25.5 | 60.9 | 9,100 | 9,300 | 1,740 | 50 |
| General av. | ..... | ..... | ..... | ..... | ..... | 57.5 | 8,600 | 8,800 | 1,640 | ..... |
| Sept. 13 | 611 | 89 | 6.08 | 3 | 22.9 | 107.5 | 15,000 | 12,300 | 2,470 | 66 |
| Oct. 18 | 679 | 91 | 6.58 | 3 | 16.3 | 97.1 | 13,500 | 9,900 | 2,050 | 76 |
| Oct. 23 | 668 | 91 | 6.52 | 2 | 17.6 | 113.6 | 15,800 | 11,800 | 2,420 | ..... |
| General av. | ..... | ..... | ..... | ..... | ..... | 106.1 | 14,800 | 11,300 | 2,310 | ..... |

[1] Assumed 3.1 calories per gram $CO_2$ for all dates through July 9; assumed 2.9 calories per gram $CO_2$ for Sept. 13, Oct. 18, and Oct. 23.

[2] Steer had about 13 kg. hay per day, Nov. 27 to Dec. 1, inclusive; 10.8 kg. Dec. 2 and 3; 5.4 kg. Dec. 4.

[3] Weight on Dec. 9; not weighed on Dec. 5.

[4] Steer had 4.5 kg. hay Jan. 9; 2.3 kg. Jan. 10.

[5] Steer had 4.5 kg. hay May 6; 2.3 kg. May 7.

[6] Steer had 9.1 kg. hay May 13; 3.4 kg. May 14; 4.5 kg. May 15; no grain.

[7] Steer had 9.1 kg. hay May 20 and 21; 4.5 kg. hay May 22; no grain.

[8] Steer had 9.1 kg. hay per day, but no grain, July 1 to 7, inclusive; 4.5 kg. hay and 0.9 kg. grain July 8 (the first day when feeding of grain began).

ing factor of a 48-hour fasting experiment on May 8–9, however, the actual amount of hay consumed during the week of May 6 to 12 was very low, and it was not until May 13 that the feed-intake settled down to an amount (7.5 kg. of water-free substance on the average) containing essentially double the metabolizable energy of the feed-intake during the submaintenance period.

Owing to the somewhat irregular method of feeding this animal, special attention must be given to the intake of hay prior to the experiments of May 16, May 23, and June 2. The special feeding program for steer 10 has already been considered in detail in discussing his increase in body-weight (see p. 98), but it is desirable to repeat here that the amounts of hay as actually consumed by this animal for the first few days in the realimentation period were as follows: on May 6, 4.5 kg.; May 7, 2.3 kg.; May 8, none; May 9, 11.3 kg.; May 10, 9.3 kg.; May 11, 4.4 kg.; and May 12, 8.8 kg. As can be seen from footnote 6 in Table 71, the amounts consumed on subsequent days were as follows: May 13, 9.1 kg.; May 14, 3.4 kg.; and May 15 (the day prior to the respiration experiment of May 16), 4.5 kg. It was noticed that irregularity in eating always disturbed digestion for a day or two, as indicated by the degree of eagerness with which the animals ate. Therefore, the use of steer 10 for a rather prolonged fasting experiment on May 8–9 complicated the conditions of feeding somewhat. Indeed, his whole rationing was quite irregular up to May 20, but on the average the water-free substance in hay consumed daily between May 6 and May 12 was 5.6 kg., and from May 13 to May 23 about 7.1 kg. Consequently, it is safe to say that prior to May 16 steer 10 was not on a very high hay ration, and at first sight this fact might serve to explain the small increase in the carbon-dioxide production from 48.9 grams on May 8 to 57.2 grams on May 16. But even on May 23 we find a relatively low value for the carbon-dioxide production of 57.5 grams per half hour, although this experiment was preceded by 2 days, May 20 and May 21, when the steer received a full maintenance amount of hay, namely, 9.1 kg. (as eaten) per day, and by 1 day, May 22 (the day before the respiration experiment) when he had half of this amount at the early morning feed, as usual. Similarly, on May 30 and May 31 he ate 9.1 kg. of hay, and but 4.5 kg. on June 1, the day before the experiment of June 2. Here again, even this full maintenance ration resulted in an almost inappreciable alteration in the carbon-dioxide production on June 2. Consequently, the reaction of steer 10 to the ingestion of hay was without doubt much less intense than that of the other steers. Grain and hay both were eaten on July 8, but as the next experiment was July 9, only the morning feed of 4.5 kg. of hay and 0.9 kg. of grain was given on July 8, and therefore the influence of so small a quantity of grain could hardly be expected to increase markedly the carbon-dioxide production. Later on in the fall, during heavy feeding with hay and grain, however, on September 13 and on subsequent dates the carbon-dioxide production had again increased enormously. The special point to be noted in connection with this series of tests with steer 10 is that on May 16 there was not a striking increase in the carbon-dioxide production following the increased feeding with hay, and that throughout the refeeding period up to and including July 9 the reaction of this animal to the increased hay ration was not at all comparable to the reactions of steers 1, 3, and 7.

The chart for steer 10 (Fig. 33) likewise shows that the extra feed did not stimulate his metabolism to the degree that it did with the other animals. The long-continued hay ration, which changed from about 4.1 kg. (water-free substance) on the average at the end of the submaintenance period to about 7.5 kg. during the refeeding period, raised the metabolism but slightly and affected the body-weight but little. As a matter of fact, although the body-

weight instantly increased somewhat on May 16, it remained practically unaltered thereafter up to July 9, at the end of the refeeding period with hay alone, and the increase in weight on May 16 is probably explained in part by the increased amount of fill due to the larger hay ration. The average heat-production per square meter of body-surface was 1,450 calories per 24 hours during the lowest part of the submaintenance period and for the subsequent hay period it was 1,640 calories, with one extremely low value of 1,350 calories occurring on June 23. From Fig. 33 it is seen that although the metabolizable energy in the feed was increased perceptibly after May 13 to an amount almost double that formerly given, this increase in feed did not result in a continually increasing body-weight. After the initial increase of about 30 kg., which occurred very rapidly, the body-weight remained constant at about 490 kg. as long as the hay ration was given, i. e., until July 8, when with the addition of grain there was a steady increase in body-weight, such as was noted with the other steers.

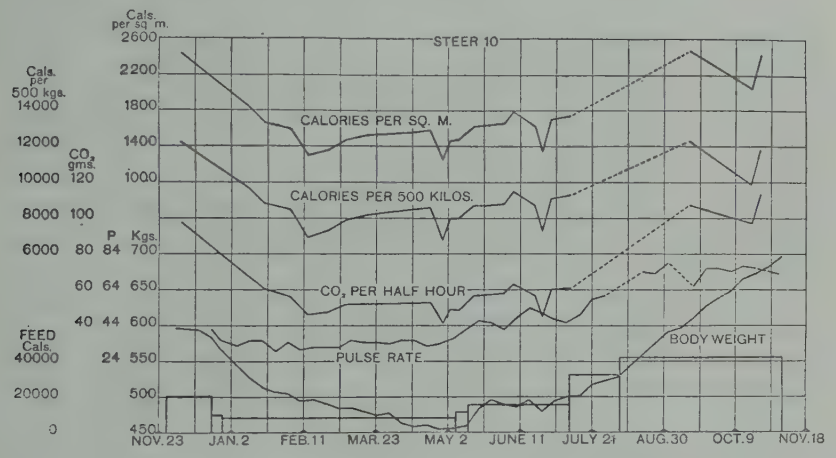


FIG. 33.—Curves for body-weight, pulse-rate per minute, carbon-dioxide production per half hour, and heat-production per 500 kg. of body-weight per 24 hours and per square meter of body-surface per 24 hours, and blocks for metabolizable energy in feed per day, steer 10. Steer 10 was fed back on hay alone from May 6 to July 8, on which date he began to receive both hay and grain.

At this point it is not possible to consider advantageously the caloric intake and output, but it is interesting to note at least in the case of steer 10 that even when the energy intake was almost doubled there was no material alteration in the body-weight. The total heat-production increased, it is true, but only from 7,800 calories per 24 hours to 8,600 calories on the average, i. e., a 10 per cent increase. In other words, an increase in feed of approximately 80 per cent increased the total heat-production but about 10 per cent and did not increase the body-weight at all, except on the very first few days. With steer 10 the special hay feeding presents many most interesting, unsolved problems.

### THE COURSE OF THE STANDARD METABOLISM OF STEER 11.

The fifth animal of Group II subjected to a reduction in ration of somewhat more than 50 per cent was steer 11, and the details of the metabolism measure-

ments for this animal are given in Table 72 and in the accompanying chart, Fig. 34. All the characteristic phenomena with regard to the percentage of empty weight, the body-surface, and the temperature of the apparatus are

TABLE 72.—*Body-weight, body-surface, pulse-rate, and standard heat-production per 24 hours, steer 11.*

| Date. | Live weight. | Per cent empty weight ($W$) to live weight. | Body-surface ($0.1186\ W^{.56}$). | No. of periods. | Average temperature of chamber. | Average carbon dioxide produced per half hour. | Heat (computed) per 24 hours. | | | Average pulse-rate per minute. |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | Total. | Per 500 kg. | Per square meter. | |
| 1918–19. | *kg.* | | *sq. m.* | | *°C.* | *gm.* | *cal.* | *cal.* | *cal.* | |
| Dec. 5[1] | [2]520 | 89 | 5.50 | 3 | ..... | 73.6 | 11,000 | 10,600 | 2,000 | .... |
| Jan. 13[3] | 460 | 88 | 5.06 | 1 | 8.0 | 89.9 | 13,400 | 14,600 | 2,650 | 33 |
| Jan. 21 | 443 | 88 | 4.94 | 2 | 15.2 | 70.6 | 10,500 | 11,900 | 2,130 | 32 |
| Jan. 27 | 446 | 88 | 4.95 | 2 | 15.8 | 61.6 | 9,200 | 10,300 | 1,860 | 36 |
| Feb. 8 | 437 | 88 | 4.90 | 3 | 13.5 | 44.0 | 6,500 | 7,400 | 1,330 | 34 |
| Feb. 18 | 427 | 87 | 4.79 | 3 | 11.4 | 47.0 | 7,000 | 8,200 | 1,460 | 31 |
| Feb. 25 | 422 | 87 | 4.75 | 3 | 13.8 | 47.1 | 7,000 | 8,300 | 1,470 | 32 |
| Mar. 5 | 418 | 87 | 4.73 | 3 | 17.3 | 43.9 | 6,500 | 7,800 | 1,370 | 33 |
| Mar. 10 | 406 | 86 | 4.61 | 3 | 15.8 | 41.3 | 6,100 | 7,500 | 1,320 | 32 |
| Apr. 15 | 386 | 86 | 4.46 | 3 | 14.1 | 44.5 | 6,600 | 8,500 | 1,480 | 36 |
| Apr. 22 | 380 | 86 | 4.42 | 3 | 17.1 | 51.3 | 7,600 | 10,000 | 1,720 | 37 |
| Apr. 30[4] | 386 | 86 | 4.46 | 3 | 17.9 | 44.6 | 6,600 | 8,500 | 1,480 | 34 |
| General av. | ..... | ..... | ..... | ... | ..... | 53.3 | 7,900 | 9,400 | 1,660 | .... |
| Average, Feb. 8–Apr. 30 | ..... | ..... | ..... | ... | ..... | ..... | ..... | ..... | 1,460 | .... |
| May 13[5] | 425 | 87 | 4.78 | 3 | 18.6 | 69.6 | 9,700 | 11,400 | 2,030 | 52 |
| May 21[6] | 432 | 87 | 4.83 | 3 | 20.5 | 68.4 | 9,500 | 11,000 | 1,970 | 58 |
| June 2 | 451 | 87 | 4.95 | 3 | 28.1 | 80.5 | 11,200 | 12,400 | 2,260 | 56 |
| June 9 | 419 | 87 | 4.74 | 3 | 19.4 | 84.7 | 11,800 | 14,100 | 2,490 | 68 |
| June 19 | 428 | 87 | 4.79 | 3 | 22.9 | 78.2 | 10,900 | 12,700 | 2,280 | 59 |
| June 23 | 428 | 87 | 4.79 | 3 | 20.9 | 87.0 | 12,100 | 14,100 | 2,530 | 59 |
| June 28 | 471 | 89 | 5.16 | 1 | 21.8 | 89.9 | 12,500 | 13,300 | 2,420 | 63 |
| July 10 | 503 | 89 | 5.38 | 3 | 22.9 | 94.1 | 13,100 | 13,000 | 2,430 | 63 |
| July 14 | 503 | 89 | 5.38 | 3 | 26.4 | 85.6 | 11,900 | 11,800 | 2,210 | 63 |
| Sept. 9 | 587 | 90 | 5.97 | 3 | 22.6 | 103.0 | 14,300 | 12,200 | 2,400 | 63 |
| Sept. 15 | 599 | 91 | 6.09 | 3 | 19.9 | 115.1 | 16,000 | 13,400 | 2,630 | 63 |
| Oct. 18 | 629 | 91 | 6.27 | 3 | 18.5 | 103.2 | 14,400 | 11,400 | 2,300 | 70 |
| Oct. 23 | 615 | 91 | 6.19 | 3 | 18.6 | 102.7 | 14,300 | 11,600 | 2,310 | 70 |
| General av. | ..... | ..... | ..... | ... | ..... | 89.4 | 12,400 | 12,500 | 2,330 | .... |

[1] Steer had about 9 kg. hay per day Nov. 27 to Dec. 3, inclusive; 4.8 kg. Dec. 4.
[2] Weight on Dec. 9; not weighed on Dec. 5.
[3] Steer had 3.6 kg. hay Jan. 11; 1.5 kg. Jan. 12.
[4] Steer had 3.6 hay Apr. 28; 1.8 kg. Apr. 29.
[5] Steer had 3.6 kg. hay May 5; 7.3 kg. May 6; 7.1 kg. May 7; 8.9 kg. May 8; 8.8 kg. May 9; 7.9 kg. May 10; 5.4 kg. May 11; 4.7 kg. May 12.
[6] Steer had 5.4 kg. hay and 3.2 kg. grain May 17; 5.2 kg. hay and 3.2 kg. grain May 18; 10.2 kg. hay and 3.2 kg. grain May 19; 2.0 kg. grain May 20, and finished eating hay not eaten May 19.

seen with this animal as with the others. The normal value on December 5 for the carbon-dioxide production is considerably less than that found on January 13, approximately 3 weeks after the curtailment in ration, but although the value for January 13 is based upon one period only and is seem-

ingly very high, no justification for ruling it out appeared in a close examination of the protocols. The course of the carbon-dioxide production of steer 11 during the submaintenance period is similar to that of the other animals in Group II. On May 13, after a week on an increased hay ration, a great increase in this factor is observed. The records show that the amount of hay received by steer 11 was doubled on May 6. Thus, on May 5 he ate 3.6 kg. of hay, while on May 6 he ate 7.3 kg. Thereafter the amount eaten was from 7 to 9 kg., until 2 days before the respiration experiment on May 13. Steer 11 had therefore been subsisting upon a relatively large amount of hay prior to this experiment.

The total 24-hour heat-production is 11,000 calories with normal feeding on December 5. On January 13, in spite of a pronounced reduction in weight of 60 kg., the total heat-production increases to 13,400 calories, a very high value found in the one period acceptable for this day. Thereafter there is the usual decrease, a level of about 6,500 calories being reached on February 8 and held constant until after the experiment of April 30. The heat-production per 500 kg. of body-weight is 10,600 calories per 24 hours at the start, increases to a high value on January 13, and then decreases to a level of about 8,000 calories during the submaintenance period, with one inexplicably high value on April 22 of 10,000 calories. With realimentation the heat-production per 500 kg. rises immediately to 11,000 calories or over and remains at a high figure for the rest of the period of observation. As already seen, we are inclined to lay more stress upon the heat-production per square meter of body-surface, as indicating with ruminants a possibly better representation of the morphological law of growth. Examining the computations on this basis, we find that at the start, in December, the heat-production is 2,000 calories per square meter of body-surface per 24 hours. There is a high value on January 13, corresponding to the other high metabolism values, and thereafter there is a steady decrease to a low average value of 1,460 calories, with an increase immediately after realimentation and with values well up toward 2,300 and 2,400 calories at the end. In general, the course of the metabolism and the course of the body-weight of steer 11 are distinctly the same as those noted with the preceding steers throughout the entire period, except steer 10, with which animal the effect of hay feeding was unusual. It is to be recalled, however, that steer 10 was the only one of Group II that did not receive grain at the beginning of the realimentation period.

The average values for the submaintenance period are as follows: 53.3 grams of carbon dioxide per half hour, 7,900 calories per 24 hours, 9,400 calories per 500 kg. of body-weight per 24 hours, and 1,660 calories per square meter of body-surface per 24 hours. These averages include, however, a period of transition during the first three experiments. At the low submaintenance level, February 8 to April 30, inclusive, the average 24-hour heat production is 1,460 calories per square meter of body-surface. With realimentation all the metabolism values increase enormously. The average carbon-dioxide production is 89.4 grams per half hour, the total 24-hour heat-production rises to an average of 12,400 calories, the heat-production per 500 kg. of body-weight per 24 hours rises to 12,500 calories, and that per square meter of body-surface to 2,330 calories. These average values are again in full accord with the results obtained with steers 1, 3, 7, and 10.

The curves for steer 11 in Fig. 34 call for no special comment, as they simply visualize the results recorded in Table 72, although on the chart we have the additional information with regard to the metabolizable energy of the feed.

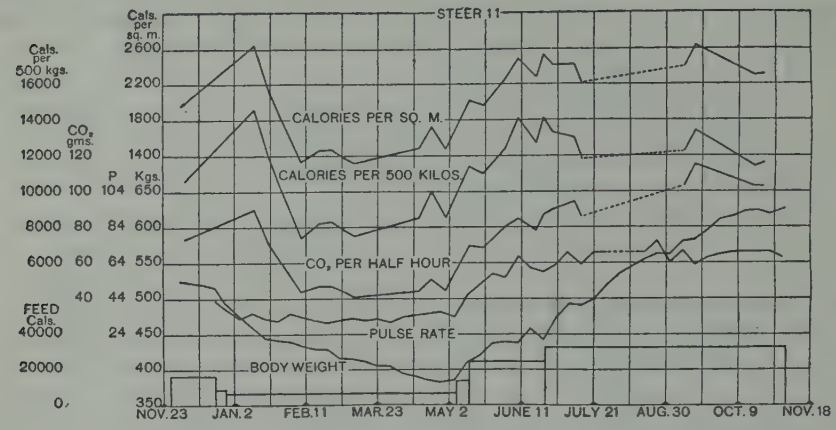


FIG. 34.—Curves for body-weight, pulse-rate per minute, carbon-dioxide production per half hour, and heat-production per 500 kg. of body-weight per 24 hours and per square meter of body-surface per 24 hours, and blocks for metabolizable energy in feed per day, steer 11.

## GENERAL CONCLUSIONS REGARDING THE INFLUENCE OF UNDERNUTRITION ON THE STANDARD METABOLISM OF ANIMALS SUBSISTING ON A RATION SOMEWHAT LESS THAN 50 PER CENT OF THEIR MAINTENANCE REQUIREMENT, GROUP II.

The discussion of the metabolism of Group II as a whole may be divided into three distinct sections: first, the course of the metabolism during the maintenance period; second, that during the submaintenance period; and third, that during realimentation. With realimentation 4 of the 5 steers were given fattening rations, while the fifth, steer 10, was retained upon a supposedly maintenance ration of hay for several months, followed by fattening rations. For the purpose of comparing all these animals, obviously the total 24-hour heat-production may not be used, owing to the wide differences in body-weight. Of the two other methods of comparison in which attempts are made to equalize differences in the size of the animals, namely, that on the basis of 500 kg. of body-weight and that on the basis of surface-area, we have selected the latter method and have incorporated in Table 73 a comparison of the standard 24-hour heat-production per square meter of body-surface of all 5 animals of Group II, giving the average values for the several important feeding-periods. Although this table and subsequent similar tables are confined to a comparison of the heat-production per square meter of body-surface, an examination of the individual charts for the several animals will show that very little difference is to be observed in the comparison of the same animals at different periods, whether the comparison is made upon the basis of 500 kg. of body-weight or upon the basis of surface-area. In Table 73 the standard metabolism for four different periods of the year is recorded: first, for the maintenance period in December, when but one experiment was made with each steer; second, for the entire submaintenance period; third, for

the low level of the submaintenance period, eliminating the adjustment period of the first few weeks; and finally, the entire refeeding period from May 6 to October 29, inclusive.

Attention has already been called to the uniformity of the December values, that is, the maintenance values. Although there is a wide range from 1,900 calories per square meter of body-surface to 2,430 calories, the general average value for this group of animals is 2,120 calories, or essentially that of the control group (steers 2, 4, and 5), i. e., 2,080 calories. It has already been pointed out (see p. 259) that the average normal value for this period of maintenance should really be made up not of those obtained with the 3 control animals alone, but of those obtained with all 14 animals, since all the steers were upon essentially the same nutritive plane prior to the curtailments in ration. Considering the submaintenance period as a whole, we find a very great fall in the heat-production per square meter of body-surface, which now ranges from

TABLE 73.—*Standard heat-production per square meter of body-surface per 24 hours on different planes of nutrition, Group II.*

(Average values based on data given in Tables 68, 69, 70, 71, and 72.)

| Plane of nutrition. | Steer 1. | Steer 3. | Steer 7. | Steer 10. | Steer 11. | General average. |
|---|---|---|---|---|---|---|
| | *cal.* | *cal.* | *cal.* | *cal.* | *cal.* | *cal.* |
| Hay maintenance[1] | 1,900 | 2,260 | 2,000 | 2,430 | 2,000 | 2,120 |
| Submaintenance on hay[2] | 1,610 | 1,670 | 1,650 | 1,510 | 1,660 | 1,620 |
| Low level of submaintenance on hay[3] | 1,390 | 1,530 | 1,460 | 1,450 | 1,460 | 1,460 |
| Fattening with hay and grain[4] | 2,100 | 2,170 | 2,110 | [5]2,310 | 2,330 | 2,200 |
| Age | 4 yrs. 8 mos. | 3 yrs. 8 mos. | 2 yrs. 8 mos. | 5 yrs.+ | 3 yrs. 8 mos. | 3 yrs. 11 mos. |

[1] Represents one value only, secured in Dec., 1918.
[2] Represents entire period of submaintenance on hay.
[3] Represents 5 to 9 values for each steer secured from Feb. to May, 1919.
[4] Represents data secured between May 6 and Oct. 29, 1919.
[5] This average represents only 3 values secured in Sept. and Oct. Steer 10 was fed back on hay alone from May 6 to July 7, inclusive, and his standard heat-production during this time was 1,640 cals.

1,510 calories with steer 10 to 1,670 calories with steer 3. The general average is 1,620 calories, which is very much less than the average of 2,120 calories noted for the normal level in December. If we eliminate the period of adjustment in the first few weeks of the submaintenance period and consider only the last few months, we find that the level is still lower, averaging 1,460 calories with considerable uniformity, the range being from 1,390 calories with steer 1 to 1,530 calories with steer 3. This low level of submaintenance was sustained with practically all these animals for a period of about 3 months, and represents the submaintenance level more distinctly than does the average value for the entire period. During the refeeding period from May 6 to October 29 the average values range from 2,100 calories with steer 1 to as high as 2,330 calories with steer 11. The general average for the entire group is 2,200 calories. The difference between the low level of metabolism during submaintenance, namely, 1,460 calories, and 2,200 calories, the metabolic level during the fattening period, is tremendous, the increase in metabolism amounting to somewhat over 50 per cent.

A comparison of these results with those for the control steers is of importance. We have already seen that the general average value on maintenance

rations is essentially the same with Group II as that with the 3 control steers. We have now to compare the general average value obtained with Group II during the low submaintenance period of approximately 3 months, namely, 1,460 calories, with that obtained with steers 2, 4, and 5 during the long maintenance period on hay only, namely, 1,820 calories. In this comparison we must disregard, for the moment at least, the low average minimum value of 1,470 calories found with the control group, a value not measurably different from the 1,460 calories noted with our submaintenance animals at their low level, since the low metabolic level observed with the control animals was only for a period of about 2 or 3 weeks, while with Group II the low level was maintained for 3 months or over. Furthermore, we may hardly compare the low submaintenance level of 1,460 calories with the maintenance level in December of 2,120 calories, but we should more properly compare this low level of 1,460 calories with the average value of 1,820 calories for the control group of animals during the corresponding long period of hay maintenance. From this comparison it is clear that a curtailment in ration amounting to somewhat more than 50 per cent lowered the standard metabolism from 1,820 calories per square meter per 24 hours to 1,460 calories, a markedly different metabolic plane being thus established. It is advisable at this point to emphasize the fact that the steers in Group II were fed only enough to carry them through the winter, and that consequently on the reduced hay ration they actually subsisted on but slightly less than one-half of what they needed when on the full hay ration. It is obvious that without any further consideration this fact alone suggests a great economy in the energy relations of these animals on submaintenance. The general average value found with Group II during fattening, namely, 2,200 calories, is essentially the same as that obtained with the control group of animals, Nos. 2, 4, and 5, under conditions of fattening, namely, 2,160 calories.

The steers in Group II, therefore, were living upon at least three different, clearly established nutritive planes: first, the maintenance level in December, when the average 24-hour heat-production per square meter of body-surface was 2,120 calories; second, the low submaintenance level during February, March, and April, represented by the average value of 1,460 calories per square meter of body-surface; and third, the high level during the refeeding period, from May to October, when the average 24-hour heat-production per square meter of body-surface was 2,200 calories. Under ordinary conditions the animals would probably have been studied either on the first nutritive plane, that is, during maintenance in December, or on the last nutritive plane, i. e., during fattening. It is hardly probable that, as metabolism measurements are ordinarily made, the average maintenance value of 1,820 calories found with steers 2, 4, and 5, during hay feeding would be found as representative of the standard metabolism. Unquestionably the long confinement, and possibly the continuous, unvaried hay ration, contributed toward a lowering of metabolism with the control group to this low level of 1,820 calories. While, therefore, the evidence is clear that with the controls, Nos. 2, 4, and 5, the metabolic level varies from 1,820 calories during the prolonged period of hay maintenance (with a hint of one extraordinarily low level of 1,470 calories for a period of 2 or 3 weeks) to 2,160 calories during the fattening period, with the steers subsisting upon a ration somewhat less than 50 per

cent of the maintenance requirement (Group II) there is a definitely established low level of 1,460 calories for 3 months and, at the other extreme, a high level of 2,200 calories during several months of refeeding.

In the observations on steer 10 (see Table 71, p. 273), we have evidence of still another nutritive plane, for during the period from May 6 to July 8, when the animal was upon a ration of hay alone somewhat less than the initial maintenance feed-level, the heat-production per square meter of body-surface per 24 hours rose from an average value of 1,450 calories during the lowest period of submaintenance to an average value of 1,640 calories during this hay period. Thus, with steer 10 there are five different metabolic levels, although the first level in December, 2,430 calories, is essentially that noted during the fattening period. This high value of 2,430 calories was found, however, upon one day only, and hence may represent an experimental error. But at least three different metabolic levels are clearly established—in the submaintenance period, in the period of realimentation with hay alone, and finally, in the period of hay and grain.

The picture exhibited by the 5 members of Group II is strikingly uniform, therefore, the only unusual feature being that of steer 10, which, when realimentation began, was not fed with hay and grain as were the others, but was kept upon a somewhat increased hay ration with an entirely different reaction in metabolism under these conditions. The important conclusion to be drawn from the measurements with Group II is that we have to deal not with one or two, but probably a large and varying number of metabolic levels, depending upon the state of nutrition of the animal itself.

Although the computation of the heat-production per square meter of body-surface is supposed by most writers to equalize all animals, it can be seen how erroneous the conception of a general value for the heat-production per square meter of body-surface for all animals under *all* conditions must be. To be sure, certain writers have insisted that the animals should be in the same nutritive condition. The exact explanation of this expression is very difficult to make. Kellner[a] states that the law of surface-area and heat-production loses its value as a result of prolonged withdrawal of food, during which time the composition of the body is essentially altered, and that only with animals in approximately the same nutritive condition as, for example, after one day's withdrawal of food, is the relationship between heat-production and body-surface shown. When our first 12 animals were studied in the same condition of nutrition, namely, in December, they were found as a group to have essentially the same heat-production per square meter of body-surface. When the 5 steers in Group II, together with 2 steers of the control group, were studied during the fattening period, the average values for the heat-production per square meter of body-surface were likewise essentially constant. The individual differences noted under both conditions, however, still make the existence of a surface-area law very problematical.

### METABOLISM AS AFFECTED BY TWO SUCCESSIVE CURTAILMENTS IN RATION OF APPROXIMATELY 40 AND 60 PER CENT, GROUP III.

Since the general picture of the influence of undernutrition upon the metabolism was so strikingly uniform with all the 5 individual members of

[a] Kellner, Die Ernährung der landw. Nutztiere, Berlin, 1920, 9th ed., p. 99.

Group II and a preliminary survey of the results obtained with Group III shows a reasonable degree of uniformity, we may treat this group in a somewhat more abbreviated manner and consider both the tables and the charts as a whole rather than consider each one separately. The first curtailed ra-

TABLE 74.—*Body-weight, body-surface, pulse-rate, and standard heat-production per 24 hours, steer 6.*

| Date. | Live weight. | Per cent empty weight (W) to live weight. | Body-surface ($0.1186W^{2/3}$). | No. of periods. | Average temperature of chamber. | Average carbon dioxide produced per half hour. | Heat (computed)[1] per 24 hours. | | | Average pulse-rate per minute. |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | Total. | Per 500 kg. | Per sq. meter. | |
| 1918–19. | *kg.* | | *sq. meters* | | *°C.* | *gm.* | *cal.* | *cal.* | *cal.* | |
| Dec. 7[2] | [4]435 | 88 | 4.88 | 3 | ..... | 66.3 | 9,900 | 11,400 | 2,030 | ..... |
| Jan. 14[4] | 409 | 87 | 4.66 | 3 | 11.5 | 62.2 | 9,300 | 11,400 | 2,000 | 35 |
| Jan. 22 | 401 | 87 | 4.61 | 3 | 13.2 | 56.8 | 8,500 | 10,600 | 1,840 | 37 |
| Jan. 28 | 392 | 87 | 4.54 | 4 | 11.1 | 59.6 | 8,900 | 11,400 | 1,960 | 39 |
| Feb. 5[5] | 390 | 87 | 4.52 | 5 | 13.7 | 49.6 | 7,400 | 9,500 | 1,640 | 35 |
| General av. | ..... | ..... | ..... | ..... | ..... | 57.1 | 8,500 | 10,700 | 1,860 | ..... |
| Feb. 11[6] | 388 | 87 | 4.52 | 3 | 10.2 | 35.4 | 5,300 | 6,800 | 1,170 | 31 |
| Feb. 19 | 375 | 86 | 4.39 | 3 | 10.9 | 43.7 | 6,500 | 8,700 | 1,480 | 32 |
| Feb. 26 | 369 | 86 | 4.34 | 3 | 14.2 | 38.4 | 5,700 | 7,700 | 1,310 | 33 |
| Mar. 4 | 362 | 86 | 4.29 | 3 | 15.6 | 42.3 | 6,300 | 8,700 | 1,470 | 33 |
| Mar. 10 | 356 | 86 | 4.24 | 3 | 12.7 | 35.8 | 5,300 | 7,400 | 1,250 | 35 |
| Apr. 9 | 345 | 85 | 4.13 | 3 | 15.8 | 41.1 | 6,100 | 8,800 | 1,480 | 34 |
| Apr. 19 | 342 | 85 | 4.11 | 3 | 13.4 | 45.1 | 6,700 | 9,800 | 1,630 | 34 |
| Apr. 24 | 340 | 85 | 4.09 | 3 | 15.0 | 38.2 | 5,700 | 8,400 | 1,390 | 36 |
| May 2 | 340 | 85 | 4.09 | 3 | 18.0 | 34.0 | 5,100 | 7,500 | 1,250 | 35 |
| May 7[7] | 345 | 85 | 4.13 | 3 | 16.4 | 38.2 | 5,700 | 8,300 | 1,380 | 39 |
| General av. | ..... | ..... | ..... | ..... | ..... | 39.2 | 5,800 | 8,200 | 1,380 | ..... |
| May 16[8] | 372 | 86 | 4.36 | 2 | 16.5 | 54.1 | 8,100 | 10,900 | 1,860 | 58 |
| May 28 | 358 | 86 | 4.26 | 2 | 20.9 | 61.1 | 9,100 | 12,700 | 2,140 | 55 |
| June 21 | 400 | 87 | 4.60 | 3 | 24.2 | 63.1 | 9,400 | 11,800 | 2,040 | 67 |
| June 26 | 402 | 87 | 4.61 | 3 | 24.2 | 67.3 | 10,000 | 12,400 | 2,170 | 65 |
| July 8 | 430 | 88 | 4.84 | 3 | 22.0 | 67.7 | 10,100 | 11,700 | 2,090 | 63 |
| Sept. 16 | 450 | 88 | 5.00 | 3 | 17.5 | 71.5 | 10,600 | 11,800 | 2,120 | 57 |
| Oct. 20 | 470 | 88 | 5.13 | 3 | 16.0 | 60.4 | 9,000 | 9,600 | 1,750 | 57 |
| Oct. 27 | 471 | 88 | 5.13 | 3 | 18.7 | 70.7 | 10,500 | 11,100 | 2,050 | 63 |
| General av. | ..... | ..... | ..... | ..... | ..... | 64.5 | 9,600 | 11,500 | 2,030 | ..... |

[1] Assumed 3.1 cals. per gram $CO_2$ for all dates.

[2] Steer had 6.9 kg. hay Dec. 4; 7.4 kg. Dec. 5; 3.6 kg. Dec. 6.

[3] Weight on Dec. 9; not weighed on Dec. 7.

[4] Steer had 5.0 kg. hay Jan. 11; 4.9 kg. Jan. 12; 2.7 kg. Jan. 13.

[5] Steer had 5.3 kg. hay Feb. 3; 2.5 kg. Feb. 4.

[6] Steer had 3.1 kg. hay Feb. 9; 1.5 kg. Feb. 10.

[7] Steer had 3.2 kg. hay per day May 1 to 5, inclusive. On May 6 he was supposed to begin receiving a full maintenance ration of 10 kg. of hay per day, but since he was used for a respiration experiment on May 7, he received on May 6 only 4.8 kg. hay in the morning and the evening feed was withheld.

[8] Steer had 9.8 kg. hay May 12; 5.0 kg. May 13; 4.1 kg. May 14; 2.3 kg. May 15; and 2.2 kg. May 16; steer went on pasture May 13 and amount of hay fed gradually decreased; no hay after May 16; steer kept on pasture until Oct. 29, but received some hay after Oct. 5; brought back from pasture and given both hay and grain, Oct. 29 to Nov. 3, inclusive.

tion with Group III was designed to be a compromise between the ration received by the control group and that received by Group II (a ration somewhat less than one-half the maintenance amount), as we were somewhat uncertain with regard to the exact fate of animals subjected to such a drastic curtailment in ration as were the steers in Group II. Consequently, after the

preliminary maintenance-level of metabolism was measured, Group III was subjected on December 22 to a curtailment in ration amounting to approximately 40 per cent of their supposed maintenance ration. On February 8, when it was seen that all the steers were doing very well, a second curtailment in ration was made amounting to about 60 per cent of the original maintenance

TABLE 75.—*Body-weight, body-surface, pulse-rate, and standard heat-production per 24 hours, steer 8.*

| Date. | Live weight. | Per cent empty weight ($W$) to live weight. | Body-surface ($0.1186W^{2/3}$). | No. of periods. | Average temperature of chamber. | Average carbon dioxide produced per half hour. | Heat (computed) per 24 hours. | | | Average pulse-rate per minute. |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | Total. | Per 500 kg. | Per sq. meter. | |
| 1918–19. | *kg.* | | *sq. meters* | | *°C.* | *gm.* | *cal.* | *cal.* | *cal.* | |
| Dec. 6[1] | [2]466 | 89 | 5.13 | 3 | ..... | 78.1 | 11,600 | 12,400 | 2,260 | ..... |
| Jan. 14[3] | 414 | 88 | 4.73 | 3 | 10.8 | 70.9 | 10,500 | 12,700 | 2,220 | 36 |
| Jan. 22 | 421 | 88 | 4.78 | 3 | 16.5 | 55.0 | 8,200 | 9,700 | 1,720 | 34 |
| Jan. 28 | 412 | 88 | 4.72 | 2 | 14.2 | 57.7 | 8,600 | 10,400 | 1,820 | 34 |
| General av. | ..... | ..... | ..... | ..... | ..... | 61.2 | 9,100 | 10,900 | 1,920 | ..... |
| Feb. 10[4] | 399 | 87 | 4.59 | 3 | 12.1 | 46.4 | 6,900 | 8,600 | 1,500 | 33 |
| Feb. 18 | 381 | 87 | 4.46 | 3 | 9.2 | 52.7 | 7,800 | 10,200 | 1,750 | 34 |
| Mar. 5 | 368 | 86 | 4.33 | 3 | 16.0 | 47.5 | 7,100 | 9,600 | 1,640 | 33 |
| Mar. 12 | 371 | 86 | 4.36 | 3 | 12.9 | 47.2 | 7,000 | 9,400 | 1,610 | 36 |
| Apr. 11 | 341 | 85 | 4.10 | 3 | 15.7 | 44.1 | 6,600 | 9,700 | 1,610 | 35 |
| Apr. 19 | 337 | 85 | 4.07 | 3 | 16.2 | 47.0 | 7,000 | 10,400 | 1,720 | 33 |
| Apr. 28 | 345 | 85 | 4.13 | 3 | 18.2 | 45.0 | 6,700 | 9,700 | 1,620 | 35 |
| May 2[5] | 344 | 85 | 4.12 | 2 | 18.1 | 47.5 | 7,100 | 10,300 | 1,720 | 35 |
| General av. | ..... | ..... | ..... | ..... | ..... | 47.2 | 7,000 | 9,700 | 1,650 | ..... |
| May 12[6] | 369 | 86 | 4.34 | 3 | 18.1 | 57.5 | 8,600 | 11,700 | 1,980 | 43 |
| May 21[7] | 381 | 87 | 4.46 | 2 | 20.3 | 65.2 | 9,100 | 11,900 | 2,040 | 69 |
| May 29 | 408 | 87 | 4.66 | 3 | 25.4 | 81.1 | 11,300 | 13,800 | 2,420 | ..... |
| June 6 | 403 | 87 | 4.62 | 2 | 28.0 | 78.0 | 10,900 | 13,500 | 2,360 | 80 |
| June 21 | 404 | 87 | 4.62 | 3 | 27.8 | 83.1 | 11,600 | 14,400 | 2,510 | 72 |
| June 27 | 447 | 89 | 5.00 | 3 | 28.6 | 100.7 | 14,000 | 15,700 | 2,800 | 80 |
| July 9 | 464 | 89 | 5.12 | 3 | 21.1 | 92.5 | 12,900 | 13,900 | 2,520 | 79 |
| Sept. 8 | 547 | 91 | 5.75 | 3 | 26.7 | 103.7 | 14,400 | 13,200 | 2,500 | ..... |
| Sept. 13 | 544 | 91 | 5.73 | 3 | 20.8 | 95.7 | 13,300 | 12,200 | 2,320 | 75 |
| Oct. 16 | 561 | 92 | 5.88 | 3 | 21.0 | 95.9 | 13,300 | 11,900 | 2,260 | 72 |
| Oct. 22 | 552 | 92 | 5.82 | 3 | 18.5 | 74.8 | 10,400 | 9,400 | 1,790 | 68 |
| Oct. 31 | 567 | 92 | 5.92 | 3 | 19.5 | 104.0 | 14,500 | 12,800 | 2,450 | 72 |
| General av. | ..... | ..... | ..... | ..... | ..... | 86.0 | 12,000 | 12,900 | 2,330 | ..... |

[1] Steer had 10 to 12 kg. hay per day Nov. 27 to Dec. 4, inclusive; 4.9 kg. Dec. 5.
[2] Weight on Dec. 9; not weighed on Dec. 6.
[3] Steer had 5.4 kg. hay Jan. 12; 2.7 kg. Jan. 13.
[4] Steer had 3.2 kg. hay Feb. 8; 1.5 kg. Feb. 9.
[5] Steer had 3.2 kg. hay Apr. 30; 1.5 kg. May 1.
[6] Steer had 8.1 kg. hay May 8; 9.3 kg. May 9; 6.4 kg. May 10; on May 11 no hay given, but steer finished eating hay not eaten May 10.
[7] Steer had 10.9 kg. hay and 3.2 kg. grain May 17; 5.4 kg. hay and 3.2 kg. grain May 18 and 19, respectively; on May 20 steer had 2.0 kg. grain and no new hay given, but steer finished eating hay not eaten May 19.

ration. In other words, the ration actually received amounted to about 40 per cent of the original maintenance ration. The steers were kept at this level until May 6, when all were given essentially double the amount of hay then being fed, the ration thus being brought back not quite to the level of the original maintenance quantity. Group III differs, therefore, from Group II in that it was subjected successively to two different, substantial curtail-

ments in ration, finally subsisting upon an actual daily feed measurably less in proportion to the maintenance ration than that received by Group II during submaintenance. Although in apportioning the animals among the three groups, I, II, and III, every effort was made to secure distinctly repre-

TABLE 76.—*Body-weight, body-surface, pulse-rate, and standard heat-production per 24 hours, steer 9.*

| Date. | Live weight. | Per cent empty weight ($W$) to live weight. | Body-surface ($0.1186W^{.56}$). | No. of periods. | Average temperature of chamber. | Average carbon dioxide produced per half hour. | Heat (computed)[1] per 24 hours. | | | Average pulse-rate per minute. |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | Total. | Per 500 kg. | Per sq. meter. | |
| 1918–19. | *kg.* | | *sq. meters* | | *°C.* | *gm.* | *cal.* | *cal.* | *cal.* | |
| Dec. 6[2] | [3]574 | 87 | 5.76 | 4 | ..... | 85.0 | 12,600 | 11,000 | 2,190 | ..... |
| Jan. 15[4] | 524 | 87 | 5.44 | 3 | 11.4 | 72.6 | 10,800 | 10,300 | 1,990 | 37 |
| Jan. 23 | 523 | 87 | 5.44 | 3 | 16.3 | 60.1 | 8,900 | 8,500 | 1,640 | 38 |
| Jan. 29 | 533 | 87 | 5.50 | 3 | 12.6 | 60.1 | 8,900 | 8,300 | 1,620 | 40 |
| Feb. 4[5] | 528 | 87 | 5.47 | 2 | 14.9 | 57.8 | 8,600 | 8,100 | 1,570 | 39 |
| General av. | ..... | ..... | ..... | ..... | ..... | 62.7 | 9,300 | 8,800 | 1,710 | ..... |
| Feb. 10[6] | 518 | 87 | 5.41 | 3 | 13.3 | 47.5 | 7,100 | 6,900 | 1,310 | 37 |
| Feb. 20 | 514 | 87 | 5.38 | 3 | 10.8 | 51.5 | 7,700 | 7,500 | 1,430 | 35 |
| Mar. 3 | 500 | 86 | 5.25 | 3 | 17.3 | 54.7 | 8,100 | 8,100 | 1,540 | 36 |
| Mar. 11 | 479 | 85 | 5.07 | 2 | 15.8 | 48.5 | 7,200 | 7,500 | 1,420 | 36 |
| Apr. 16 | 455 | 84 | 4.87 | 3 | 15.1 | 43.2 | 6,400 | 7,000 | 1,310 | 37 |
| Apr. 19 | 458 | 84 | 4.90 | 3 | 17.7 | 52.5 | 7,800 | 8,500 | 1,590 | 37 |
| Apr. 29 | 454 | 84 | 4.87 | 3 | 16.9 | 50.7 | 7,500 | 8,300 | 1,540 | 38 |
| May 3[7] | 455 | 84 | 4.87 | 2 | 15.8 | 48.6 | 7,200 | 7,900 | 1,480 | 38 |
| General av. | ..... | ..... | ..... | ..... | ..... | 49.7 | 7,400 | 7,700 | 1,450 | ..... |
| May 13[8] | 477 | 84 | 5.02 | 2 | 18.3 | 82.6 | 12,300 | 12,900 | 2,450 | 64 |
| May 22[9] | 454 | 84 | 4.87 | 3 | 18.4 | 82.7 | 12,300 | 13,500 | 2,530 | 64 |
| May 29 | 459 | 84 | 4.91 | 3 | 21.9 | 81.1 | 12,100 | 13,200 | 2,460 | 62 |
| June 7 | 475 | 84 | 5.01 | 1 | 27.5 | 80.4 | 12,000 | 12,600 | 2,400 | 70 |
| June 21 | 518 | 85 | 5.32 | 3 | 26.4 | 76.0 | 11,300 | 10,900 | 2,120 | ..... |
| June 26 | 526 | 85 | 5.38 | 3 | 26.6 | 77.0 | 11,500 | 10,900 | 2,140 | 67 |
| July 8 | 564 | 85 | 5.61 | 3 | 24.2 | 87.6 | 13,000 | 11,500 | 2,320 | 68 |
| July 14 | 551 | 85 | 5.53 | 3 | 23.0 | 92.2 | 13,700 | 12,400 | 2,480 | 68 |
| Sept. 16 | 575 | 86 | 5.73 | 3 | 19.0 | 71.2 | 10,600 | 9,200 | 1,850 | 60 |
| Oct. 17 | 606 | 86 | 5.92 | 3 | 18.8 | 74.9 | 11,100 | 9,200 | 1,880 | ..... |
| Oct. 24 | 601 | 86 | 5.89 | 3 | 17.7 | 74.2 | 11,000 | 9,200 | 1,870 | 54 |
| General av. | ..... | ..... | ..... | ..... | ..... | 80.0 | 11,900 | 11,400 | 2,230 | ..... |

[1] Assumed 3.1 cals. per gram $CO_2$ for all dates.
[2] Steer had 10 to 13 kg. hay per day Nov. 27 to Dec. 4, inclusive; 5.2 kg. Dec. 5.
[3] Weight on Dec. 9; not weighed on Dec. 6.
[4] Steer had 6.2 kg. hay Jan. 13; 2.8 kg. Jan. 14.
[5] Steer had 6.4 kg. hay Feb. 2; 3.2 kg. Feb. 3.
[6] Steer had 4.3 kg. hay Feb. 8; 2.2 kg. Feb. 9.
[7] Steer had 4.3 kg. hay May 1; 2.2 kg. May 2.
[8] Steer had 12.2 kg. hay May 9; 10.9 kg. May 10; 6.4 kg. May 11; 5.4 kg. May 12.
[9] Steer put on pasture May 13 and amount of hay fed gradually decreased; no hay after May 16; steer kept on pasture until Oct. 29, but received some hay after Oct. 5; brought back from pasture and given both hay and grain, Oct. 29 to Nov. 3, inclusive.

sentative groups both as regards age, condition, and habit of feeding, it is a fact that Group III as a whole was somewhat inferior in condition to either Group I or II (see p. 223), inasmuch as the animals were scored a little lower in practically all cases than those in Groups I and II. The age-factor in all groups was balanced essentially alike, for both young and old animals were

included. However, the fact that Group III was scored a little lower than Group II influenced us in not subjecting these steers at first to quite so drastic a curtailment of ration.

The usual series of metabolism measurements were made with these 4 animals, Nos. 6, 8, 9, and 12, exactly as with the other steers, and the data are

TABLE 77.—*Body-weight, body-surface, pulse-rate, and standard heat-production per 24 hours, steer 12.*

| Date. | Live weight. | Per cent empty weight ($W$) to live weight. | Body-surface ($0.1186W^{\frac{2}{3}}$). | No. of periods. | Average temperature of chamber. | Average carbon dioxide produced per half hour. | Heat (computed) per 24 hours. | | | Average pulse-rate per minute. |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | Total. | Per 500 kg. | Per sq. meter. | |
| 1918–19. | *kg.* | | *sq. meters* | | °*C.* | *gm.* | *cal.* | *cal.* | *cal.* | |
| Dec. 5[1] | [2]401 | 87 | 4.61 | 4 | ..... | 61.9 | 9,200 | 11,500 | 2,000 | ..... |
| Jan. 15[3] | 352 | 86 | 4.22 | 2 | 11.5 | 61.8 | 9,200 | 13,100 | 2,180 | 38 |
| Jan. 24[4] | 356 | 86 | 4.24 | 2 | 14.6 | 56.6 | 8,400 | 11,800 | 1,980 | 36 |
| Jan. 29 | 365 | 86 | 4.31 | 3 | 14.9 | 45.4 | 6,800 | 9,300 | 1,580 | 37 |
| General av. | ..... | ..... | ..... | ..... | ..... | 54.6 | 8,100 | 11,400 | 1,910 | ..... |
| Feb. 11[5] | 340 | 86 | 4.12 | 3 | 7.4 | 45.0 | 6,700 | 9,900 | 1,630 | 35 |
| Feb. 24 | 321 | 85 | 3.95 | 3 | 12.0 | 33.4 | 5,000 | 7,800 | 1,270 | 29 |
| Mar. 8 | 324 | 85 | 3.97 | 4 | 12.6 | 46.7 | 6,900 | 10,600 | 1,740 | 30 |
| Mar. 13 | 323 | 85 | 3.97 | 3 | 13.1 | 37.8 | 5,600 | 8,700 | 1,410 | 31 |
| Apr. 15 | 298 | 84 | 3.74 | 3 | 15.4 | 37.4 | 5,600 | 9,400 | 1,500 | 30 |
| Apr. 23 | 293 | 84 | 3.70 | 3 | 16.0 | 41.9 | 6,200 | 10,600 | 1,680 | 31 |
| Apr. 30 | 288 | 84 | 3.66 | 3 | 17.3 | 31.0 | 4,600 | 8,000 | 1,260 | 30 |
| May 4[6] | 297 | 84 | 3.73 | 3 | 16.8 | 30.2 | 4,500 | 7,600 | 1,210 | 30 |
| General av. | ..... | ..... | ..... | ..... | ..... | 37.9 | 5,600 | 9,100 | 1,460 | ..... |
| May 14[7] | 330 | 85 | 4.01 | 3 | 22.2 | 70.4 | 9,800 | 14,800 | 2,440 | 56 |
| May 23 | 332 | 85 | 4.03 | 2 | 18.2 | 66.2 | 9,200 | 13,900 | 2,280 | 60 |
| June 3 | 343 | 86 | 4.15 | 3 | 23.6 | 70.3 | 9,800 | 14,300 | 2,360 | 69 |
| June 9 | 334 | 86 | 4.08 | 2 | 17.7 | 62.7 | 8,700 | 13,000 | 2,130 | 69 |
| June 19 | 369 | 86 | 4.34 | 3 | 26.4 | 72.3 | 10,100 | 13,700 | 2,330 | 68 |
| June 23 | 347 | 86 | 4.17 | 3 | 22.7 | 67.7 | 9,400 | 13,500 | 2,250 | 68 |
| July 10 | 382 | 87 | 4.46 | 3 | 23.6 | 69.1 | 9,600 | 12,600 | 2,150 | 68 |
| Sept. 11 | 477 | 89 | 5.21 | 2 | 22.7 | 93.4 | 13,000 | 13,600 | 2,500 | 73 |
| Sept. 15 | 475 | 89 | 5.19 | 3 | 21.6 | 88.1 | 12,300 | 12,900 | 2,370 | 73 |
| Oct. 17 | 501 | 89 | 5.37 | 3 | 20.4 | 90.1 | 12,500 | 12,500 | 2,330 | ..... |
| Oct. 22 | 503 | 89 | 5.38 | 3 | 18.4 | 72.0 | 10,000 | 9,900 | 1,860 | ..... |
| Oct. 31 | 518 | 89 | 5.48 | 3 | 19.9 | 79.2 | 11,000 | 10,600 | 2,010 | 72 |
| General av. | ..... | ..... | ..... | ..... | ..... | 75.1 | 10,500 | 12,900 | 2,250 | ..... |

[1] Steer had 8 to 10 kg. hay per day Nov. 27 to Dec. 2, inclusive; 7.6 kg. Dec. 3; 3.9 kg. Dec. 4.
[2] Weight on Dec. 9; not weighed on Dec. 5.
[3] Steer had 4.3 kg. hay Jan. 13; 1.8 kg. Jan. 14.
[4] Steer had 4.5 kg. hay Jan. 22; 2.2 kg. Jan. 23.
[5] Steer had 2.7 kg. hay Feb. 9; 1.4 kg. Feb. 10.
[6] Steer had 2.7 kg. hay May 2; 1.4 kg. May 3.
[7] Steer had 7.5 kg. hay May 10; 5.0 kg. hay May 11; 8.8 kg. hay May 12; 5.0 kg. hay and 0.9 kg. grain May 13.

incorporated in Tables 74 to 77 herewith, as well as in the corresponding charts, Figs. 35 to 38. While the analysis of these data might proceed much along the lines of the analysis for Group II, we will consider them as a whole, pointing out, however, certain essential differences which occasionally occur.

But one normal value was obtained with Group III, in early December, as indicated in each of the tables. The first cut in ration occurred December 22.

In practically all cases there was no material decrease in heat-production nearly a month later, namely, January 14 and 15, but during the next 2 or 3 weeks there was a distinct tendency for the total heat-production to fall off

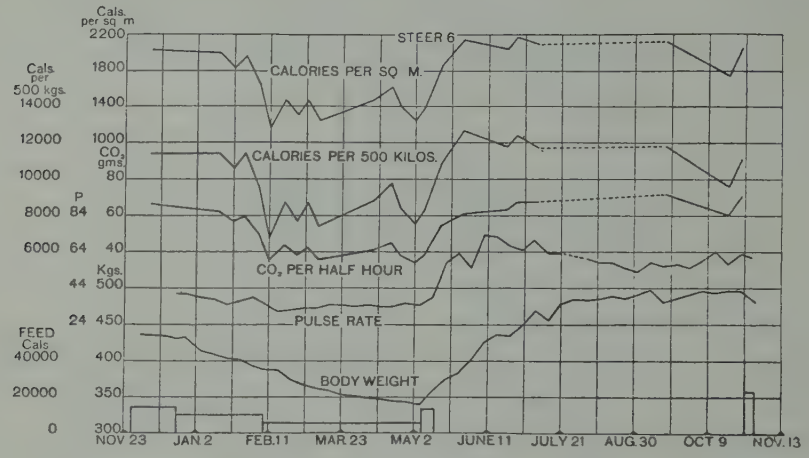


FIG. 35.—Curves for body-weight, pulse-rate per minute, carbon-dioxide production per half hour, and heat-production per 500 kg. of body-weight per 24 hours and per square meter of body-surface per 24 hours, and blocks for metabolizable energy in feed per day, steer 6. Steer 6 was put out to pasture on May 13 and received hay and grain only from October 29 to November 3; therefore no data are available for the metabolizable energy in feed during the pasture period.

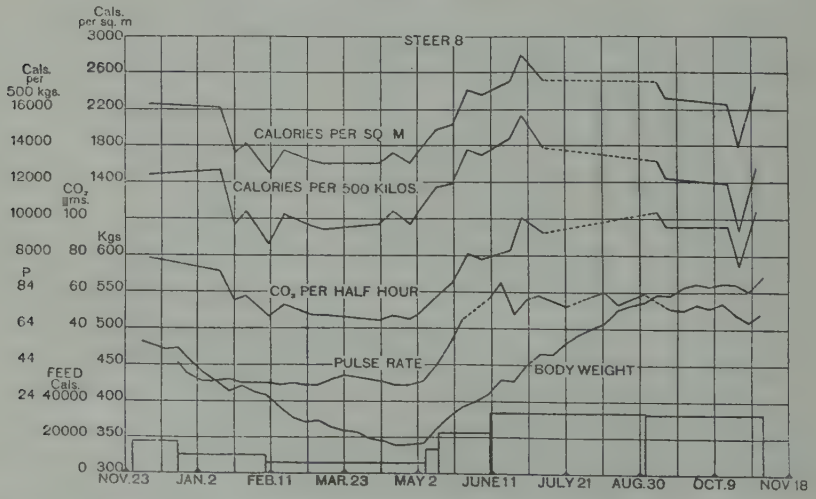


FIG. 36.—Curves for body-weight, pulse-rate per minute, carbon-dioxide production per half hour, and heat-production per 500 kg. of body-weight per 24 hours and per square meter of body-surface per 24 hours, and blocks for metabolizable energy in feed per day, steer 8.

until the time of the second curtailment of ration, February 8. The first experiment following this second curtailment showed almost invariably a noticeable drop in metabolism. The period of the first curtailment of ration,

that is, from December 22 to February 7, inclusive, thus corresponded almost identically to the period of adjustment noted with all the individual animals in Group II, which, it will be recalled, showed a sliding scale of metabolism, decreasing continually for the first four or five experimental dates. With

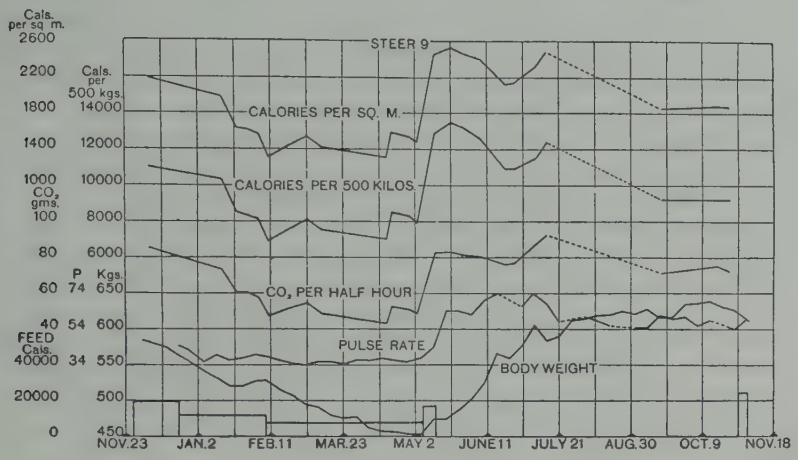


FIG. 37.—Curves for body-weight, pulse-rate per minute, carbon-dioxide production per half hour, and heat-production per 500 kg. of body-weight per 24 hours and per square meter of body-surface per 24 hours, and blocks for metabolizable energy in feed per day, steer 9. Steer 9 was put out to pasture on May 13 and received hay and grain only from October 29 to November 3; therefore no data are available for the metabolizable energy in feed during the pasture period.

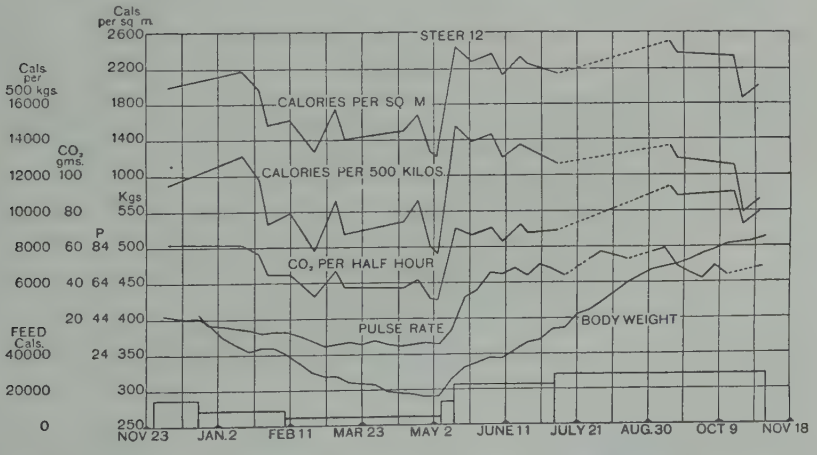


FIG. 38.—Curves for body-weight, pulse-rate per minute, carbon-dioxide production per half hour, and heat-production per 500 kg. of body-weight per 24 hours and per square meter of body-surface per 24 hours, and blocks for metabolizable energy in feed per day, steer 12.

Group III there was a similar decrease. In practically all cases the minimum level starts with the first experiment after February 8, and from then on the total heat-production remains essentially constant in the case of each steer. Since there was almost invariably a still further decrease in body-weight during

this second or lowest level of feeding, there is a slight tendency for the heat-production per 500 kg. of body-weight to increase from the beginning to the end of this period, although this is less noticeable with steer 12 than with any of the others.

With the resumption of the heavier hay ration, consisting usually of double the last submaintenance amount, there is at once a striking increase in all metabolism factors with all of the animals. This increase is least with steer 8, but even with this animal there was an actual rise in the total 24-hour heat-production from 7,100 to 8,600 calories. With steer 9 the increase is tremendous, i. e., from 7,200 calories on May 3 to 12,300 calories on May 13. Likewise, steer 12 shows a metabolism more than doubled, i. e., from 4,500 to 9,800 calories in 10 days between experiments at this period of the year. Following the first few days of refeeding on hay alone, 2 of these animals, Nos. 6 and 9, were turned out to pasture, and although metabolism measurements were secured from time to time as they were brought in from pasture, no data with regard to the amount of feed consumed are available until October 29, when both steers were brought back from pasture and given hay and grain for the last 6 days of observation. The precise amount of feed ingested by steers 6 and 9, therefore, is unknown for the greater part of the refeeding period. While the course of the metabolism up to the time of refeeding is essentially uniform with all of these 4 animals, rather striking differences subsequent to refeeding are noted, some of them very difficult to explain. For example, with steer 6 the total heat-production after May 16 continues to increase, although at a rather slow rate, while with steer 9 (also put out to pasture) the total heat-production after May 13 remains reasonably constant throughout the entire period of refeeding, and, indeed, at a very high level.

These animals should be compared, however, with reference to body-weight or body-surface. On the basis of the heat-production per 500 kg. of body-weight, the metabolism of steer 6 does show a tendency to stay at a level of about 12,000 calories after May 28, while the metabolism of steer 9 by this method of computation distinctly falls off from May 13 to the end of the experimental period. The course of the metabolism of the other animals, Nos. 8 and 12, is practically identical with that noted with the steers in Group II, with which they may most properly be compared, so far as their feeding program is concerned. Finally, we can refer for the moment to the computations per square meter of body-surface. On this basis the high initial level, the sliding scale for the first three or four experiments during the first ration curtailment, the low level for the 3 months from February 8 to May 12, and the striking increase following the refeeding, are characteristic for all of the animals.

The average standard 24-hour heat-production per square meter of body-surface during the main feeding-periods is summarized in Table 78 for Group III. Reference has already been made to the fact that the general average value of 2,120 calories obtained for steers 6, 8, 9, and 12 during maintenance feeding in December is practically identical with the general averages observed with the two other groups, i. e., 2,080 calories with Group I and 2,120 calories with Group II. During the period from December 22 to February 7, inclusive, that is, the period of adjustment, the average heat-production per square meter

is 1,850 calories. This value is not directly referable to any average values for Groups I and II, since with these two groups the averages for this preliminary period have not been made, and we can pass immediately to the low level from February 8 to May 5, when the steers in Group III were on a ration amounting to about 40 per cent of the original maintenance ration. At this level the general average is 1,490 calories, comparable to the low level with Group II of 1,460 calories and to the low level of 1,470 calories noted with Group I for 2 or 3 weeks. In the fattening period the metabolism rises to a high level of 2,210 calories on the average for all 4 animals, a value very close to that of 2,200 calories noted with Group II and 2,160 calories noted with Group I, the control group. Since steers 6 and 9 were on pasture and not given grain until October 29, i. e., after all the respiration experiments had been made, it may be questioned whether their results should be included in the general average for the fattening period. If they were omitted from

TABLE 78.—*Standard heat-production per square meter of body-surface per 24 hours on different planes of nutrition, Group III.*

[Average values, based on data given in Tables 74, 75, 76, and 77.]

| Plane of nutrition. | Steer 6. | Steer 8. | Steer 9. | Steer 12. | General average. |
|---|---|---|---|---|---|
| | *cal.* | *cal.* | *cal.* | *cal.* | *cal.* |
| Hay maintenance[1] | 2,030 | 2,260 | 2,190 | 2,000 | 2,120 |
| Submaintenance on hay[2] | 1,860 | 1,920 | 1,710 | 1,910 | 1,850 |
| Low level of submaintenance on hay[3] | 1,380 | 1,650 | 1,450 | 1,460 | 1,490 |
| Fattening with hay and grain[4] | [5]2,030 | 2,330 | [5]2,230 | 2,250 | 2,210 |
| Age | 2 yrs. 8 mos. | 3 yrs. 8 mos. | 5 yrs.+ | 2 yrs. 5 mos. | 3 yrs. 5 mos. |

[1] Represents one value only, secured in December 1918.
[2] Dec. 22, 1918, to Feb. 7, 1919, inclusive.
[3] Feb. 8 to May 5, 1919, inclusive.
[4] May 12 to Oct. 31, 1919, inclusive.
[5] Represents data secured chiefly while steers 6 and 9 were on pasture. These steers were at pasture from May 13 to Oct. 28, inclusive; on May 13 to 16 and Oct. 5 to Nov. 3 they also received some hay and from Oct. 29 to Nov. 3 a small amount of grain.

the average, the result would be increased to 2,290 calories. As steer 9 has shown such a pronounced reaction to pasturage, however, we have felt it wiser to retain both values in the general average.

As stated at the beginning of the discussion of Group III, the picture shown by each member of the group is so characteristic for the whole and agrees so perfectly with the general trend of the influence of submaintenance rations upon metabolism exhibited in Group II that exactly the same conclusions may be drawn: first, that this group as a whole showed an initial maintenance metabolism corresponding to that of all the other steers; second, that the first curtailment of ration was accompanied by a slow depression of metabolism corresponding to that noted with Group II in the period of adjustment; third, that after the second curtailment of ration a low metabolic plane was established and held for several months; and finally, that with realimentation either on hay and grain or on pasture there was a striking increase in metabolism, and a level essentially the same as the initial level of the December experiments was reached.

### A COMPARISON OF THE COURSE OF THE STANDARD METABOLISM OF THE CONTROL STEERS IN GROUP I WITH THAT OF THE STEERS ON THE SUBMAINTENANCE RATIONS, GROUPS II AND III.

In the presentation of our metabolism data we have stressed considerably our method of computing the standard metabolism and our belief that the data, because uncontaminated, may be used for the comparison not only of animals in the same group, but particularly of the same animal, at different nutritive planes, and finally of groups of animals at different nutritive planes. We regret that the true basal metabolism, that is, the metabolism under conditions of complete muscular repose and after the active processes of digestion have ceased, could not have been measured with these animals. We feel strongly that the method of computing the basal metabolism thus far employed by other writers, namely, by measuring the metabolism after the ingestion of varying amounts of a single feedstuff and computing therefrom the basal metabolism by correcting for the estimated increase due to the feed, is fundamentally wrong. On the other hand, we realize that criticism will justly be leveled at our method of computing the standard metabolism. But whatever criticisms may be thus raised, it is clear that by the method of experimental procedure all of our groups of steers are directly comparable, and hence it is important to compare the course of their standard metabolism throughout the winter.

#### Course of the Standard Heat-production per 500 kilograms of Body-weight per 24 Hours.

The use of the values for the total heat-production per 24 hours for purposes of comparison is not legitimate, since we are dealing with groups of steers of

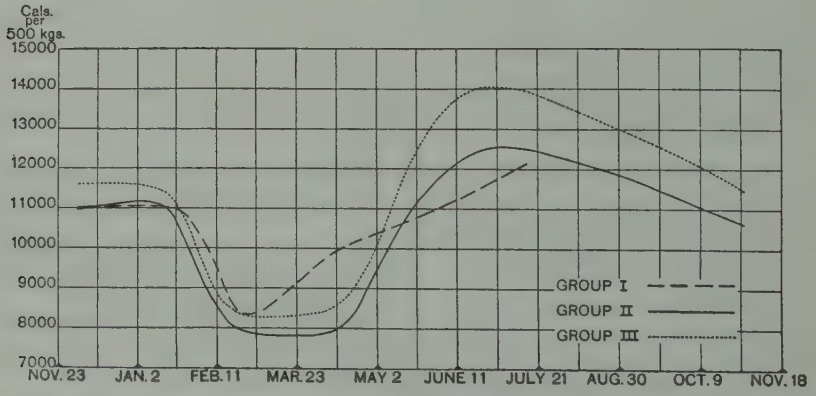


Fig. 39.—The general trend of the standard heat-production per 500 kg. of body-weight per 24 hours at different nutritive planes, Groups I, II, and III.

very different weights. We will therefore consider, first, the heat-production per 500 kg. of body-weight. To visualize better the relationships between these several groups of steers, we have plotted a curve for the 24-hour heat-production per 500 kg. of body-weight for Group II and also for Group III, exactly as was done for Group I. (See Fig. 28, p. 249). In preparing these curves, all of the individual observations for each steer in the group were

plotted on one chart and then a line representing the general trend of the metabolism was sketched through these points. Such a curve was prepared by 5 different individuals and the 5 resulting curves were ultimately blended into one general average curve. While it is a dangerous procedure to attempt to indicate the course of the metabolism by a single curve, if it is recognized that this curve is meant to represent simply a general trend, the use of such a curve may be justified. We have incorporated in Fig. 39, accordingly, the curves for the three groups, I, II, and III, representing the general trend of the heat-production per 500 kg. of body-weight per 24 hours. Strictly speaking, these three groups are comparable only until the first week in May, for thereafter the differences in the nature of the realimentation were so great that it is perhaps unjustifiable to make direct comparison. The curves, however, have been sketched for the entire period of observation, and in an attempt to make the latter portion of the curves more strictly comparable, the data for steers 2, 6, and 9 were plotted only up to the date when they went to pasture and for steer 10 only through May 12, so that the curves during the realimentation period reflect only the influence of the heavy hay and grain feeding and not the influence of pasturage or prolonged hay maintenance.

Although Groups II and III underwent a curtailment of ration on December 22, there is a distinct tendency for their metabolism to remain at a constant level until about the middle of January. Their metabolism then undergoes a very pronounced drop, reaching a low level about February 25. For the next 7 weeks the level remains unaltered, although Group III is at a little higher level than Group II. Finally, when refeeding began, there is a tremendous increase in the standard metabolism of both groups. With Group I, the control group, the noticeable depression in metabolism about the last 2 weeks in February (which has already been commented upon) must be taken as indicating but a temporary fluctuation in the metabolic level.

The salient features of these curves are (1) that Group I (the control group) shows a depression in metabolism for 2 weeks, although on a constant, supposedly maintenance ration, and (2) that with Groups II and III there is a very striking and long-continued decrease in metabolism coincident with the curtailment in ration. It is to be noted that since Group II, and especially Group III, both have a standard metabolism at the beginning averaging higher than that of Group I, the actual depression in metabolism with these two groups is even larger, when compared with Group I, than at first glance appears from the chart. Similarly the rise in metabolism following the increase in rations is very pronounced, the differences in the levels being ascribable in part to differences in the type of realimentation. A critical analysis of these curves involves obviously a consideration of the character of the feed after May 6.

Laying special stress upon that portion of the curves prior to May 2, it can be seen that the course of the standard 24-hour heat-production per 500 kg. of body-weight was alike for all three groups of steers in that after an initial period of essentially constant metabolism there was a noticeable fall. This decrease, however, was greater with the two groups on curtailed rations than with the control group. The curve for Group III does not reach the low level reached by the curve for Group II, but it will be noticed that it is on a higher level at the start, and therefore the decrease to the low level is

as great proportionately with Group III as it is with Group II. Since ultimately Group III was subjected to a ration curtailment even greater than that of Group II, it is perhaps somewhat surprising that the proportional decrease, particularly toward the end of the submaintenance period, was not even greater than that noted with Group II. The course of the curve for the control group has already been extensively discussed. It should be emphasized again, however, that in considering all of these curves one must remember that there was a very wide divergence of individual points at practically all stages, a divergence that can best be noted by reference to Fig. 28, page 249. Upon the basis of the heat-production per 500 kg. of body-weight, therefore, there is a clearly established lower metabolic level with Groups II and III than with Group I. Intelligent consideration of the course of the curves after May 2 can only be made after a closer analysis of the kinds and amounts of feed given.

### The Course of the Standard Heat-production per Square Meter of Body-surface per 24 Hours.

A further comparison of the heat-production of these three groups of steers on the basis of the heat-production per square meter of body-surface is justi-

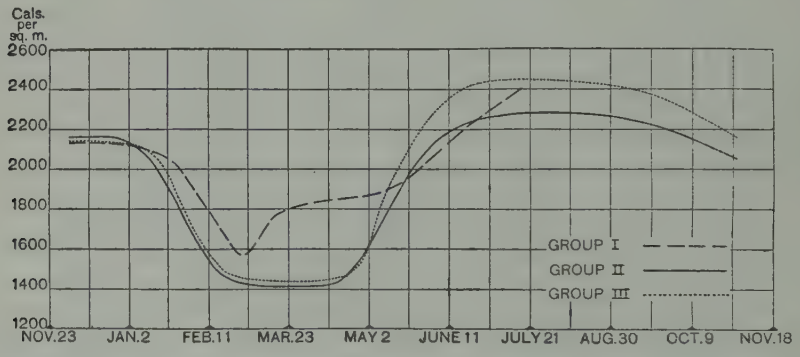


Fig. 40.—The general trend of the standard heat-production per square meter of body-surface per 24 hours at different nutritive planes, Groups I, II, and III.

fiable, and the corresponding curves for the three groups have been prepared as before by 5 different individuals and the blended curves incorporated in Fig. 40. Before laying too much emphasis upon this comparison, however, it must be reiterated that these charts are sketched upon a series of widely differing points and represent trends only, with very large deviations. Furthermore, we are by no means in sympathy with this method of computing the heat-production per square meter of body-surface, for in spite of assertions to the contrary on the part of its advocates, this method has not been divested of the fundamental belief that the heat-loss has been *determined* by the body-surface. But as an index of the general morphological law of growth, it is probable that changes in the computed surface-area (involving as it does with these ruminants the five-eighths power of the body-weight) represent a somewhat closer, more direct approximation to the true changes in organic tissue than do direct weight changes. With these reservations we are prepared to make the comparisons between the several groups.

The course of the curve for Group I has already been discussed, the somewhat inexplicably low metabolic level which existed for a short time about the end of February and the first of March, and the subsequent increase being indicated. With Groups II and III there is a very sharply defined drop in metabolism, beginning about the middle of January; a low level is reached at the end of February and held for several months; and after May 2 there is a rapid rise during the period of refeeding. In general, therefore, the three curves in Fig. 40 agree perfectly with those shown in Fig. 39, the most noticeable differences being (1) that when referred to the unit of surface-area the standard metabolism of all three groups starts at nearly the same normal level in early December, and (2) that the depression in metabolism noted in Groups II and III is even more pronounced in comparison with that in Group I than it was on the 500-kg. basis. Finally, the heat-production per square meter of body-surface shows even closer agreement with the three groups after refeeding begins than does the heat-production per 500 kg. of body-weight.

From Figs. 39 and 40, therefore, it seems quite clear that for a comparison of different groups of animals general curves based upon the calculations of the heat-production per square meter of body-surface (as computed by Moulton's formula) show greater uniformity than curves based upon the heat-production per 500 kg. of body-weight. Before accepting this conclusion as too great a proof of the uniformity in the heat-production per square meter of body-surface under like conditions, one should recognize, in the first place, that the individual variations on this basis of computation are literally tremendous, as reference to Fig. 29 for the control steers will show. Secondly, the method of computing the surface-area, although infinitely refined by Moulton, is still at best rather crude, and judging from our own experience in assessing values for Moulton's constant, $K$, with steer 1 (see p. 225) and similar animals, we think it is capable of still further refinement. We are more and more impressed with the fact that Moulton should not have overlooked the important element of skeletal growth, as exemplified by the measurement of some typical length corresponding to the height in humans. One of the most pronounced factors in the success of Du Bois in placing the measurement and computation of the surface-area of humans upon a rational basis was the fact that, unlike Meeh and other predecessors, he did not disregard body-length, i. e., height. We have searched unsuccessfully in Moulton's reports for data for major lengths. While undoubtedly such measurements were taken, they have not as yet (so far as we are aware) been published. It seems to us very clear that a method of computing the surface-area based upon the weight of the animal and not disregarding length would prove infinitely more satisfactory than the present method. Particularly is this true when one is dealing, as we were, with animals in widely varying states of nutrition, a situation that faces every stock feeder who is handling either immature animals which are to be raised to maturity and fattened, or thin, unfattened animals, purchased in the market and subsequently to be fattened. We sincerely hope that Professor Moulton and his colleagues will revise their computations, based upon measurements that they must have in their possession, and present physiologists with a materially bettered method for computing the surface-area of large domestic animals.

Although we have pointed out the fact that the heat-production per square meter of body-surface is more uniform with the three groups than the heat-production by any other method of computation, it is still important to note that the heat-production per square meter of body-surface is of itself a variant, fluctuating with the nutritive plane of the animal. When the weight is low the metabolism is low. When there is full nutrition with surfeit feeding, the metabolism is high. But still more important to recognize and more difficult to explain is the fact that the control group on constant hay feeding underwent a very pronounced change in metabolic level, at one time actually reaching a point nearly as low as the low level observed with the submaintenance groups. Under the circumstances, therefore, remembering that we are not dealing here strictly with basal metabolism, but with standard metabolism under conditions approximating those outlined in Armsby's consideration of the metabolism per 24 hours, standing, we can see that the variation in metabolism is so great as to rule out completely any conception of a uniform standard metabolism for animals that will obtain under all conditions.

### METABOLISM AS AFFECTED BY A CURTAILMENT IN RATION OF APPROXIMATELY 60 PER CENT, GROUP IV.

The whole investigation at this point in its chronological course, namely, at the end of the first year's work, showed a number of missing factors, particularly evidence with regard to the efficiency of the hay ration for maintenance of protein or nitrogenous equilibrium. Consequently, a second year's intensive series of experiments was planned with 2 other animals, steers A and B (Group IV).

The primary object of the observations with Group IV was to make a complete study of the nitrogen balance and to determine the digestibility of the hay, for the idea has gained credence that on low rations the digestibility of the hay is materially different from what it is on full rations and that animals on a low nutritive plane are not able to digest as much as more vigorous animals.[a] Accordingly, with Group IV the curtailment in rations was carried out in a manner not unlike that with Group II. The details for Group IV, steers A and B, are given in Tables 79 and 80 and in Figs. 41 and 42. During the maintenance period both steers were given daily 9,090 grams of mixed hay of much the same chemical composition as that given to steers 1 to 12. It is particularly unfortunate that we could not profit by the experience of the preceding year and make more respiration experiments with steers A and B during the maintenance period (December 27 to January 10) but, as a matter of fact, only one respiration experiment was made with each animal, and that on January 7. On this date the total 24-hour heat-production is high, 12,600 calories with steer A and 14,400 calories with steer B, in part explained by the fact that both steers were large animals, weighing

[a] Trowbridge, Moulton, and Haigh (Univ. Missouri, Agric. Expt. Sta., Bull. 28, 1918, p. 23), in writing of their undernourished steer No. 592, say "This reduced vitality probably lessened his digestive capacity so that he could not digest his food as thoroughly as he did in the earlier part of the experiment." They state also (loc. cit., p. 21) that "the condition of the animal is a factor influencing its ability to digest its feed. The animals in the thin and unthrifty condition do not seem to be able to handle their feed as economically as the animals in better condition, in spite of the fact that the need for the nutrients is much greater."

591 and 561 kg., respectively. Their condition was about the same as that noted with most of the first year's animals at the beginning of the experiment, i. e., medium thin.

TABLE 79.—*Body-weight, body-surface, pulse-rate, and standard heat-production per 24 hours, steer A.*

| Date. | Live weight. | Per cent empty weight ($W$) to live weight. | Body-surface ($0.1186W^{\frac{2}{3}}$). | No. of periods. | Average temperature of chamber. | Average carbon dioxide produced per half hour. | Heat (computed)[1] per 24 hours. | | | Average pulse-rate per minute. |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | Total. | Per 500 kg. | Per sq. meter. | |
| 1920. | *kg.* | | *sq. meters* | | *°C.* | *gm.* | *cal.* | *cal.* | *cal.* | |
| Jan. 7[2] | 591 | 89 | 5.95 | 3 | 13.6 | 84.5 | 12,600 | 10,700 | 2,120 | 49 |
| Jan. 19[3] | 562 | 88 | 5.73 | 3 | 3.3 | 61.8 | 9,200 | 8,200 | 1,610 | 34 |
| Feb. 3 | 554 | 88 | 5.68 | 3 | 14.3 | 44.3 | 6,600 | 6,000 | 1,160 | 35 |
| Feb. 28 | 540 | 88 | 5.58 | 3 | 5.0 | 70.4 | 10,500 | 9,700 | 1,880 | 36 |
| Mar. 6 | [4]536 | 88 | 5.56 | 2 | 18.5 | 63.1 | 9,400 | 8,800 | 1,690 | 36 |
| Mar. 19 | 517 | 87 | 5.40 | 3 | 13.6 | 58.6 | 8,700 | 8,400 | 1,610 | 34 |
| Mar. 30 | 506 | 87 | 5.32 | 3 | 16.7 | 55.8 | 8,300 | 8,200 | 1,560 | 37 |
| Apr. 13 | 498 | 87 | 5.27 | 3 | 16.0 | 54.9 | 8,200 | 8,200 | 1,560 | 34 |
| Apr. 28 | 488 | 87 | 5.21 | 1 | 15.5 | 58.1 | 8,600 | 8,800 | 1,650 | 36 |
| May 11 | 492 | 87 | 5.23 | 3 | 16.9 | 57.8 | 8,600 | 8,700 | 1,640 | 37 |
| May 25[5] | 460 | 86 | 4.98 | 3 | 19.4 | 53.2 | 7,900 | 8,600 | 1,590 | 41 |
| General av. | | | | | | 57.8 | 8,600 | 8,400 | 1,600 | |
| June 8[6] | 503 | 87 | 5.31 | 3 | 20.2 | 76.9 | 11,400 | 11,400 | 2,150 | 51 |
| July 13[7] | | | | 2 | 29.1 | 85.9 | 12,800 | | | |
| Aug. 30 | | | | 2 | 29.6 | 95.9 | 14,300 | | | |
| Sept. 18 | 593 | 89 | 5.97 | 3 | 19.5 | 87.2 | 13,000 | 11,000 | 2,180 | |
| Oct. 16[8] | 620 | 89 | 6.13 | 3 | 21.9 | 91.7 | 13,600 | 11,000 | 2,220 | [9]56 |
| General av. | | | | | | 87.5 | 13,000 | 11,100 | 2,180 | |
| Oct. 29[10] | 636 | 90 | 6.27 | 3 | 20.2 | 90.6 | 12,600 | 9,900 | 2,010 | 55 |
| Nov. 12 | 657 | 90 | 6.40 | 2 | 14.1 | 98.4 | 13,700 | 10,400 | 2,140 | 64 |
| Dec. 18 | 691 | 90 | 6.61 | 3 | 13.6 | 109.3 | 15,200 | 11,000 | 2,300 | 76 |
| General av. | | | | | | 99.4 | 13,800 | 10,400 | 2,150 | |

[1] Assumed 3.1 cal. per gram $CO_2$ for all dates through Oct. 16; assumed 2.9 cal. per gram $CO_2$ on Oct. 29 Nov. 12, and Dec. 18.

[2] Steer had 9,090 gm. hay Dec. 30 to Jan. 5, inclusive; had 4,545 gm. hay the morning of Jan. 6; afternoon feed Jan. 6 and morning and afternoon feed Jan. 7 withheld because of respiration experiments.

[3] Steer had 4,545 gm. hay Jan. 16 and 17, respectively; had 2,272 gm. hay in morning, Jan. 18; afternoon feed Jan. 18 and morning feed Jan. 19, withheld because of respiration experiment; loss made up on afternoon of Jan. 19 and morning of Jan. 20.

[4] Weight on Mar. 5; not weighed on Mar. 6.

[5] Steer had 4,000 gm. hay May 22 and 23, respectively; had 2,000 gm. hay in morning, May 24; afternoon feed May 24 and morning feed May 25 withheld because of respiration experiment, but loss made up on afternoon May 25 and morning of May 26.

[6] Steer had 9,090 gm. hay June 5 and 6, respectively; had 4,545 gm. hay in morning, June 7; afternoon feed June 7 and morning feed June 8 withheld because of respiration experiment; morning feed June 8 given immediately after respiration experiment, but feed withheld on afternoon of June 7 not made up, because steer now on full maintenance and difficult to make up loss.

[7] Steer was on pasture from June 13 to Oct. 15, inclusive.

[8] Steer had hay (amount not recorded) Oct. 16 to 21, inclusive.

[9] Represents a single value, not an average.

[10] Steer had 9,090 gm. hay, 800 gm. bran, 1,600 gm. cornmeal, Oct. 26 and 27, respectively; on morning of Oct. 28 had 4,545 gm. hay, 400 gm. bran, 800 gm, cornmeal; afternoon feed withheld because of respiration experiment.

Since we are dealing here with 2 steers living under as nearly as possible identical conditions, the comparison between the two may perhaps best be made by laying emphasis upon the charts rather than upon the tables. The

animals were the entire time in metabolism stalls, side by side, and hence were subjected to identically the same physical conditions. They had no exercise throughout the entire period other than that of walking to and from the

TABLE 80.—*Body-weight, body-surface, pulse-rate, and standard heat-production per 24 hours, steer B.*

| Date. | Live weight. | Per cent empty weight ($W$) to live weight. | Body-surface ($0.1186W^{2/3}$). | No. of periods. | Average temperature of chamber. | Average carbon dioxide produced per half hour. | Heat (computed)[1] per 24 hours. | | | Average pulse-rate per minute. |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | Total. | Per 500 kg. | Per sq. meter. | |
| 1920. | *kg.* | | *sq. meters* | | *°C.* | *gm.* | *cal.* | *cal.* | *cal.* | |
| Jan. 7[2] | 561 | 89 | 5.76 | 2 | 17.4 | 96.6 | 14,400 | 12,800 | 2,500 | 49 |
| Jan. 19[3] | 549 | 88 | 5.64 | 2 | 5.2 | 45.3 | 6,700 | 6,100 | 1,190 | 35 |
| Feb. 3 | 532 | 87 | 5.50 | 3 | 14.6 | 55.4 | 8,200 | 7,700 | 1,490 | 36 |
| Feb. 28 | 513 | 87 | 5.36 | 2 | 10.9 | 75.1 | 11,200 | 10,900 | 2,090 | 36 |
| Mar. 6 | 493 | 87 | 5.24 | 3 | 19.1 | 68.2 | 10,100 | 10,200 | 1,930 | 37 |
| Mar. 19 | 493 | 87 | 5.24 | 3 | 16.0 | 61.0 | 9,100 | 9,200 | 1,740 | 36 |
| Mar. 30 | 484 | 87 | 5.18 | 1 | 20.0 | 57.1 | 8,500 | 8,800 | 1,640 | 36 |
| Apr. 13 | 476 | 87 | 5.13 | 2 | 17.9 | 58.4 | 8,700 | 9,100 | 1,700 | 35 |
| Apr. 28 | 466 | 86 | 5.02 | 3 | 17.5 | 61.9 | 9,200 | 9,900 | 1,830 | 36 |
| May 11 | 458 | 86 | 4.97 | 3 | 17.9 | 61.8 | 9,200 | 10,000 | 1,850 | 36 |
| May 25[5] | 440 | 86 | 4.84 | 3 | 20.1 | 58.7 | 8,700 | 9,900 | 1,800 | 41 |
| General av. | ..... | ..... | ..... | ..... | ..... | 60.3 | 9,000 | 9,200 | 1,730 | ..... |
| June 8[6] | 467 | 86 | 5.03 | 3 | 22.6 | 78.0 | 11,600 | 12,400 | 2,310 | 51 |
| July 13[7] | ..... | ..... | ..... | 3 | 25.5 | 98.5 | 14,700 | ..... | ..... | ..... |
| Aug. 30 | 567 | 89 | 5.80 | 3 | 27.8 | 113.5 | 16,900 | 14,900 | 2,910 | ..... |
| Sept. 15 | 584 | 89 | 5.91 | 3 | 23.5 | 103.2 | 15,400 | 13,200 | 2,610 | ..... |
| Oct. 16[8] | 603 | 89 | 6.03 | 3 | 20.2 | 98.6 | 14,700 | 12,200 | 2,440 | [9]58 |
| General av. | ..... | ..... | ..... | ..... | ..... | 98.4 | 14,700 | 13,200 | 2,570 | ..... |
| Oct. 29[10] | 599 | 89 | 6.00 | 3 | 21.6 | 93.5 | 13,000 | 10,900 | 2,170 | 52 |
| Nov. 12 | 625 | 90 | 6.20 | 3 | 16.5 | 101.2 | 14,100 | 11,300 | 2,270 | 67 |
| Nov. 27 | 640 | 90 | 6.30 | 3 | 14.8 | 107.7 | 15,000 | 11,700 | 2,380 | 72 |
| Dec. 18 | 666 | 90 | 6.46 | 2 | 18.0 | 112.3 | 15,600 | 11,700 | 2,410 | 79 |
| General av. | ..... | ..... | ..... | ..... | ..... | 103.7 | 14,400 | 11,400 | 2,310 | ..... |

[1] Assumed 3.1 cal. per gram $CO_2$ for all dates through Oct. 16; assumed 2.9 cal. per gram $CO_2$ on Oct. 29 and subsequent dates.

[2] Steer had 9,090 gm. hay Dec. 30 to Jan. 5, inclusive; had 4,545 gm. hay the morning of Jan. 6; afternoon feed Jan. 6, and morning and afternoon feed Jan. 7 withheld because of respiration experiments.

[3] Steer had 4,545 gm. hay Jan. 16 and 17, respectively; had 2,272 gm. hay in morning, Jan. 18; afternoon feed Jan. 18 and morning feed Jan. 19 withheld because of respiration experiment; loss made up on afternoon of Jan. 19 and morning of Jan. 20.

[4] Weight on Mar. 5; not weighed on Mar. 6.

[5] Steer had 4,000 gm. hay May 22 and 23, respectively; had 2,000 gm. hay in morning, May 24; afternoon feed May 24 and morning feed May 25 withheld because of respiration experiment, but loss made up on afternoon, May 25, and morning, May 26.

[6] Steer had 9,090 gm. hay June 5 and 6, respectively; had 4,545 gm. hay in morning, June 7; afternoon feed June 7 and morning feed June 8 withheld because of respiration experiment; morning feed June 8 given immediately after respiration experiment, but feed withheld afternoon of June 7 not made up, because steer now on full maintenance and difficult to make up loss.

[7] Steer was on pasture from June 13 to Oct. 15, inclusive.

[8] Steer had hay (amount not recorded) Oct. 16 to 21, inclusive.

[9] Represents a single value, not an average.

[10] Steer had 9,090 gm. hay, 800 gm. bran, cornmeal, and cottonseed meal, respectively, Oct. 26 and 27; on morning of Oct. 28 had 4,545 gm. hay, and 400 gm. bran, linseed meal, and cottonseed meal, respectively; afternoon feed withheld because of respiration experiment.

stalls to the respiration chamber on the days when experiments were made, a distance of approximately 100 feet, but entirely under cover, as they walked simply from one wing of the barn to another.

The initial hay ration of 9,090 grams was cut on January 10 by 50 per cent. The animals therefore received 4,545 grams or about 40 per cent of the probable maintenance requirement, since the evidence seems fairly clear that the first amount of hay (9,090 grams), which was at first assumed to suffice for maintenance, actually failed to meet that condition, as the average body-weights fell off in both cases during the maintenance period and indeed more rapidly than with any of the other steers. With the curtailment of ration there was immediately a further loss of body-weight, which proceeded with both animals in a reasonably straight line, until refeeding began. With realimentation the body-weight curves (see Fig. 22, p. 97) can almost be

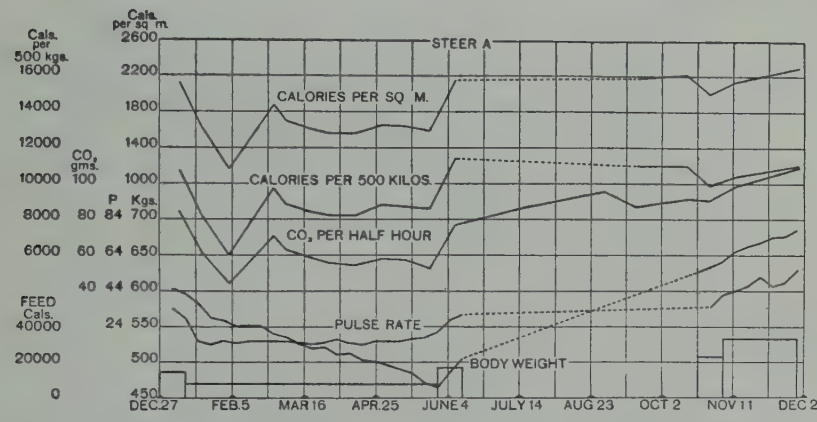


FIG. 41.—Curves for body-weight, pulse-rate per minute, carbon-dioxide production per half hour, and heat-production per 500 kg. of body-weight per 24 hours and per square meter of body-surface per 24 hours, and blocks for metabolizable energy in feed per day, steer A.

The curves for the 24-hour heat-production per 500 kg. of body-weight and per square meter of body-surface show dotted lines from June 8 to Sept. 18, although the curve for the carbon-dioxide production is a full, unbroken line. This is due to the fact that while the carbon-dioxide production was measured twice during this time, body-weight records were unfortunately overlooked, and hence the heat-production could not be computed with reference to body-weight and body-surface. Steer A was on pasture from June 13 to Oct. 15 and no daily weights were recorded during this time, except on Sept. 18 in connection with the respiration experiment, at which point the heat curves are again full, unbroken lines. The metabolizable energy in feed could not be computed for the pasture period.

superimposed, in spite of the fact that both steers were turned out to pasture on June 13, remaining there until October 15. Slight differences in the character of the grain given each steer after withdrawal from pasture are apparently not reflected in the body-weight curves. The most pronounced irregularity in the course of the several metabolism curves for steers A and B is the very low point in the curves for carbon-dioxide production and heat-production, occurring on February 3 with steer A and on January 19 with steer B. In other words, 9 days after the curtailment of ration, steer B showed absolutely the lowest values for the carbon-dioxide and heat-production noted throughout the entire experimental season, while steer A showed the lowest values about 3 weeks after the curtailment of ration. These extremely low points were followed 3 or 4 weeks later by a marked rise,

and only after this rise does the metabolism seem to take a regular course, slowly decreasing and remaining at a reasonably constant level from March 19 until the refeeding on May 29.

With the resumption of full feed the body-weight of both steers immediately increases and the carbon-dioxide production of steer A rises strikingly, remaining reasonably level from July 13 until October 15, when he was withdrawn from pasture. With the further addition of grain, the carbon-dioxide production per half hour continues to increase in the case of steer A. With steer B the situation seems quite the same as with steer A until shortly after the point of refeeding. During the refeeding period and while on pasture

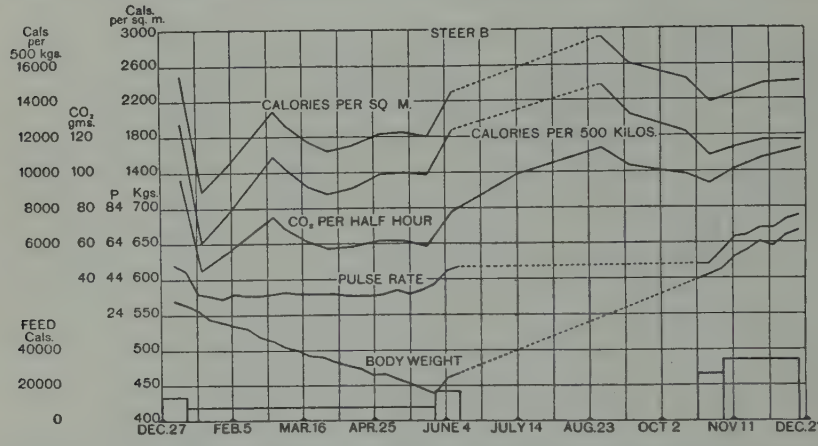


FIG. 42.—Curves for body-weight, pulse-rate per minute, carbon-dioxide production per half hour, and heat-production per 500 kg. of body-weight per 24 hours and per square meter of body-surface per 24 hours, and blocks for metabolizable energy in feed per day, steer B.

The curves for the 24-hour heat-production per 500 kg. of body-weight and per square meter of body-surface show dotted lines from June 8 to Aug. 30, although the curve for the carbon-dioxide production is a full, unbroken line. This is due to the fact that while the carbon-dioxide production was measured once during this time, the body-weight unfortunately was not recorded, and hence the heat-production could not be computed with reference to body-weight and body-surface. Steer B was on pasture from June 13 to Oct. 15 and no daily weights were recorded during this time except on Aug. 30 and Sept. 15 in connection with respiration experiments. At Aug. 30, therefore, the heat curves are again full, unbroken lines. The metabolizable energy in feed could not be computed for the pasture period.

his metabolism has a distinct tendency to increase until the last of August. There is then a decrease and the high value on August 30 is not again attained until the very last day, December 18, although in the preceding 2 months steer B was upon a heavy grain ration and making substantial gains in weight.

The course of the metabolism with both animals, as indicated by the carbon-dioxide production, is in many ways unlike that with the other submaintenance groups studied. Most striking is the very low point a few weeks after the curtailment of the ration. The second striking feature is the fact that during the realimentation period the metabolism increases very slowly after the first initial increment. Of the foregoing groups, the steers submitted more nearly to similar treatment, i. e., put upon pasture following previous

submaintenance, are steers 6 and 9. With these steers the metabolism curves are not unlike those noted with steers A and B, and the irregularities observed with steer B are quite comparable to those found with steer 9. This fact suggests that the gain in organized tissue and the activity of metabolic processes when the steer is upon pasture proceeds at a very much slower rate than when the steer is upon the high grain ration. Although steers A and B were upon fairly heavy grain rations from October 22 until December 17, during which time there was with both animals a considerable increase in body-weight (approximately 50 kg. each), it is surprising that there should have been so little increase in the metabolism.

Computations of the heat-production per 500 kg. of body-weight and per square meter of body-surface show, as is common, that the course of the two heat curves is almost parallel to that for the carbon-dioxide production per half hour. In other words, few, if any, of the irregularities disappear when the metabolism is referred to uniform conditions of weight or surface. There is, however, on all three bases of computation a definitely lower nutritive plane during the period from about the first of March to the first of June, while in the realimentation period, either with pasturage or with grain, the metabolism proceeds at a somewhat higher level. In these points these steers correspond perfectly to the earlier groups.

It would be very difficult to draw a curve showing the general trend of the metabolism of these 2 steers, owing to the scarcity and, indeed, rather wide scatter of the points, and we have hardly felt it wise to attempt such a procedure, preferring to refer directly to the general trend of the heat curves in Figs. 41 and 42, since the greater portion of these curves is essentially of the same general character, both as regards the heat-production per 500 kg. of body-weight and that per square meter of body-surface. Following a consideration of the individual values in the tables for these 2 steers, however, reference may be made with propriety to the average values obtained for several of the main periods indicating the various nutritive planes. As shown by the curves and substantiated with mathematical exactness in the tables, extraordinarily low values for the heat-production per square meter of body-surface are noted with both animals, on February 3 with steer A and January 19 with steer B. There has been a hint in many of our tables that low values are not infrequently associated with low chamber temperatures. This is true in the case of steer B, but the low metabolism of steer A on February 3 was measured when the environmental temperature was much higher than that either on January 19 or February 28. An explanation for these two extraordinarily low values is still missing.

Another feature of this series of observations with Group IV is the absence of any striking evidence of a period of adjustment during the first 4 or 5 experiments, such as was noted with Group II and with Group III during the first curtailment of ration. It might be expected that a slightly lower average would be obtained for the last 6 observations (covering 2 months) in the submaintenance period, i. e., from March 19 to May 25, but, as a matter of fact, with steer A this level would be practically the same as the average of 1,600 calories per square meter per 24 hours found for the entire submaintenance period, while with steer B the level for the last 5 or 6 obser-

vations would be slightly above the average of 1,730 calories for the entire period, owing to the fact that two extremely low values occur on the first days of experimenting in the submaintenance period. The evidence is clearly established, however, that there is a lower level of metabolism during the major portion of the submaintenance period.

TABLE 81.— *Standard heat-production per square meter of body-surface per 24 hours on different planes of nutrition, Group IV.*

[Average values, based on data given in Tables 79 and 80.]

| Plane of nutrition. | Steer A. | Steer B. | General average. | Remarks. |
|---|---|---|---|---|
| | *cal.* | *cal.* | *cal.* | |
| Hay maintenance | 2,120 | 2,500 | 2,310 | Represents one value only, secured on Jan. 7, 1920. |
| Submaintenance on hay | 1,600 | 1,730 | 1,670 | Jan. 10 to May 29, 1920. |
| Refeeding on hay and grass | 2,180 | 2,570 | 2,380 | May 29 to Oct. 22, 1920. |
| Fattening with hay and grain | 2,150 | 2,310 | 2,230 | Oct. 22 to Dec. 18, 1920. |
| Age | 3 yrs., 8 mos. | 3 yrs., 8 mos. | 3 yrs., 8 mos. | |

The refeeding period has been subdivided into two sections, the first when the animals were given hay and subsequently put on pasture, and the second when they were receiving both hay and grain. The average values for the standard 24-hour heat-production per square meter of body-surface for all of the main ration periods have been incorporated in Table 81, drawn directly from Tables 79 and 80. During the refeeding period on hay and pasture, steer B shows a high value of 2,570 calories, which seems to be caused chiefly by two high values on August 30 and September 15, as will be seen by reference to the individual figures in Table 80. No such corresponding values are noted with steer A. The general picture presented by the average figures in Table 81 is quite like that shown with the other groups of submaintenance animals. It seems unjustifiable to average the values for these 2 steers, and particularly to compare them with the averages of the other groups which have preceded them, since each of the other groups contained not less than 3 animals. While the difference of 380 calories noted in the average heat-production per square meter of body-surface with steers A and B in the maintenance period is actually exceeded by the difference between the average values for steers 1 and 10 (see Table 73, p. 279) during their maintenance period, the general average value of 2,310 calories for steers A and B is higher than the general averages of the other three groups during the maintenance period, which were remarkably uniform, i. e., 2,080, 2,120, and 2,120 calories with Groups I, II, and III, respectively. During the submaintenance period the metabolism of steers A and B averages 1,670 calories per square meter, which is considerably lower than the maintenance value of 2,310 calories and essentially the same as the average value for the entire submaintenance period with Group II, i. e., 1,620 calories, but considerably higher than the average value for the low level of submaintenance with either Group II or Group III. During the period of feeding on hay and pasturage a return to the original standard metabolism is noted, the average being 2,380 calories, and finally, with the rations of hay and grain, the level is somewhat less, 2,230 calories, but agrees remarkably well with the levels observed with the other three groups during the realimentation period.

To sum up, the standard metabolism of Group IV starts at a somewhat higher level than that of the other groups, decreases with submaintenance, but not to so low a level as in the case of Groups II and III, and returns with refeeding to essentially the original level. One can consider, therefore, that steers A and B started on a slightly higher metabolic plane than the other steers (although the dangers of this generalization have already been pointed out, since the extreme between steers A and B is not so great as that between steers 1 and 10 in Group II). In spite of the seeming irregularities in the curves as drawn in Figs. 41 and 42, the trend of the metabolism of steers A and B does conform in practically all respects to the general metabolic trends exhibited by the two preceding submaintenance groups, and therefore, we may state that each of the 11 different steers subjected to a submaintenance ration reacted in practically all particulars in conformity with the general average. We find it impossible to explain the extraordinarily low values noted with steers A and B so soon after the curtailment of ration. No one can regret any more than we do that two or three experiments each week could not have been made throughout the submaintenance period, to substantiate, if possible, these initial low values. However, since each respiration experiment under "standard metabolism" conditions involved the witholding of two feeds and a consequent temporary digestive disturbance, more than one such experiment each week was out of the question.

## GENERAL CONCLUSIONS WITH REGARD TO THE INFLUENCE OF A SUBMAINTENANCE RATION UPON METABOLISM.

Although 11 different steers were subjected to essentially the same type of ration curtailment and the metabolism curves plotted from the numerous measurements show almost identically the same general trend of metabolism under the conditions of rationing obtaining in these experiments, positive conclusions with regard to the quantitative relations between the metabolizable energy in the ration and the actual alteration in metabolism can be drawn only with a considerable degree of reserve. The wholly unexpected magnitude of the variations in the standard metabolism noted with the control group, Group I, complicated the interpretation of the results very much. It will be recalled that with Group I during the presumably maintenance hay level, there was a period of approximately 2 weeks when the standard metabolism was actually as low as the minimum standard metabolism of either Group II or Group III while subjected to ration curtailment, either on the basis of per 500 kg. of body-weight or per square meter of body-surface. This period of depression of metabolic activity, however, lasted only about 2 weeks, after which there was a rather rapid rebound to essentially the original level, which was maintained in a general way throughout the entire maintenance period with these control steers. For this great change in metabolism no definite explanation is at hand. It is coincidental with much lower temperatures in the respiration chamber, but that we have here to deal with cause and effect is by no means definitely proved, especially since all previous conceptions of the influence of environmental temperature upon metabolism would indicate an increased rather than decreased metabolic activity with low environmental temperatures. Since all three steers in the control group showed this depression in metabolism, it must be accepted as a physiological

fact. Obviously carefully planned experiments on the influence of environmental temperature must shortly be made. Indeed, it is proper to state here that such experiments are actually in progress with the apparatus at Durham. The respiration calorimeter of Armsby and Hagemann and, indeed, the large respiration chamber of Zuntz and that of Møllgaard and Andersen do not lend themselves easily to study of extremes in temperature range. Our apparatus at Durham is, however, so adjusted that we can cool it to any degree and heat it with electric heaters, and thus in its new location secure a satisfactory temperature environment.

With the 11 steers subjected to ration curtailment, the undernutrition has in every instance a pronounced influence upon the metabolism, in that after a few weeks of adjustment the metabolic level is decidedly lowered. This period of adjustment is noted with all the animals save steers A and B. The low metabolic level is maintained generally for several months until the refeeding with hay begins, when there is almost immediately a rebound in the measured metabolism, indeed, an increase not at all proportional to the increase in the metabolizable energy in the ration. Even with the heaviest fattening rations the increase in metabolism, although still continuing, is by no means proportional to the very rapid rise noted after the relatively moderate increase in the metabolizable energy in the feed immediately following the low nutritive state. As has already been pointed out in discussing the body-weight, the resumption of the original body-weight is very rapid, especially in those steers turned out to pasture, explainable, we believe, in large part by the rapid increase in fill. The metabolism of the steers on pasture likewise increases rapidly at first, but does not assume the high intensity usually noted with the grain-fed animals. Steers A and B are, however, an exception, as they do show on the average exceptionally high values during the refeeding period on hay and grass alone.

The metabolism of steers A and B was on a somewhat higher plane throughout the entire experimental year than was that of the other groups of animals. The reason for this we can not give. The nitrogen-balance test shows that there was a large loss of nitrogen throughout all the hay periods with steers A and B, a loss of nitrogen that was in all probability somewhat greater than that actually experienced (but unfortunately not measured) by steers 1 to 12. We have reason to believe that even the control animals, Nos. 2, 4, and 5, in all probability lost nitrogen. The large loss of nitrogen by steers A and B would lead us to expect a standard metabolism much lower than that of the other steers rather than higher, for it was noted with a group of humans[a] that the removal of a considerable amount of nitrogen from the body was coincidental with and possibly the cause of the depressed metabolism. But with steers A and B the metabolism was measurably above the metabolism of the other animals either per unit of weight or per unit of surface-area. Prior to ration curtailment their metabolism had been at a high level compared with that of the other animals; even during the lowest period of submaintenance their metabolism did not attain quite so low a level as that reached by the other animals; and on refeeding with hay and grass it was

[a] Benedict, Miles, Roth, and Smith, Carnegie Inst. Wash. Pub. No. 280, 1919, p. 688.

distinctly higher on the average. The higher metabolism of Group IV, even during submaintenance, is quite at variance with our conceptions with regard to the influence of undernutrition upon metabolism, drawn from work on humans. Steers A and B at the start were unquestionably on a ration somewhat below maintenance, although it was designated as "approximately maintenance." Furthermore, although we think that all of the other steers were likewise not on an absolutely maintenance ration at the start, we believe that steers A and B were on a distinctly lower ration than the others. Our reason for this belief is based, in the first place, upon the striking loss of nitrogen by steers A and B, as shown by the nitrogen-balance, and in the second place, upon the fact that there is no indication in the body-weight curve of either of these animals to show that they were approaching a constant level even at the end of the submaintenance period, a plateau of body-weight that was noticed with a large majority of the other submaintenance animals.

The discussion of the heat-production may touch upon the three different bases for comparison, namely, the total heat-production, the heat-production per 500 kg. of body-weight, and the heat-production per square meter of body-surface. All of the tables indicate without question a tremendous loss in the total heat-production at the end of the submaintenance period. In other words, the steers were actually producing not far from 40 to 50 per cent less heat than they were during the initial observations. This is to be expected, in part at least, for the simple reason that we are dealing with steers that have lost a considerable amount of weight and hence have become smaller. Employing the two standard methods of equalizing differences in body-weight, not only differences occurring in the same animal at different times but particularly differences between different animals, namely, computing the heat-production per 500 kg. of body-weight and per square meter of body-surface, we note again that in spite of the attempt to equalize differences in size of animals there is a specific metabolic depression coincidental with the submaintenance ration. Finally, the introduction into the alimentary tract of an increased amount of feed results in a stimulus to metabolism and an increase in body-weight, no matter whether the realimentation is with hay alone, as in the case of steer 10, or with pasturage alone, or with hay and grain.

The summary tables indicating the standard heat-production per square meter of body-surface at the different nutritive planes show with a regularity that can not be disregarded average values in the different groups that are rather strikingly uniform. There are in general three metabolic planes: first, that for all steers on the first day of observation on hay maintenance; second, that for Groups II, III, and IV during the long period of submaintenance feeding on hay and for Group I during the long maintenance period on hay (with Groups I, II, and III this level is subdivided further to show the lowest level noted for a portion of this period); and finally, that during the realimentation period. Thus, on the maintenance ration of hay alone the general average values for the four successive groups are respectively as follows: 2,080, 2,120, 2,120, and 2,310 calories. For the short, low level of maintenance with Group I the general average is 1,470 calories; for the long period of

low level of submaintenance, that is, ruling out the period of transition, for Groups II and III, the general averages are 1,460 and 1,490 calories; and for the entire submaintenance period with Group IV the general average is 1,670 calories. Finally, during the fattening period for all four groups the averages are 2,160, 2,200, 2,210, and 2,230 calories per square meter of body-surface per 24 hours, respectively. Under the circumstances it seems reasonably well established that the uniformity in these figures is not fortuitous, and by the measurement of the metabolic intensity of groups of animals definite nutritive planes and differences in nutritive plane of a rather high order of magnitude may be discerned.

If one considers that the steers were essentially on the same metabolic plane at the beginning of the period of hay maintenance and at the end of the fattening period, a general average value of 2,150 calories per square meter of body-surface per 24 hours would be not far from representative of the standard metabolism. The danger in accepting this general average is, however, that those results obtained during the period of hay maintenance were confined in every case to one day's observation on the animals, and, indeed, to their first experience inside the respiration chamber. Secondly, the average values found during the fattening period are made up of a series of relatively low values immediately following the ingestion of large amounts of feed, gradually increasing and culminating usually in a series of high values toward the end of the fattening period. Consequently, the average results are clearly somewhat low in general, rather than high.

This criticism does not apply, however, to the average values found with Groups II and III during the low level of submaintenance, namely, 1,460 and 1,490 calories, but here the fact that Group I, the control steers, showed an average of 1,470 calories for a period of about 2 weeks without any ration curtailment, complicates the interpretation of the results enormously. Furthermore, with Group IV, steers A and B (whose initial ration we have reason to believe was distinctly below maintenance and consequently whose curtailment of ration was probably as great as with any of the other groups), there was neither a period of adjustment nor was there the absolute minimum noted with Groups II and III, or indeed, with Group I. Under these circumstances we hardly feel like presenting an average value to represent the low level of metabolism, save with Groups II and III.

The all important fact from the physiological standpoint is, however, that the maintenance level of 2,150 calories per square meter of body-surface per 24 hours was, as a result of curtailed rations, lowered in general by about one-third, i. e., to 1,475 calories, the average for the low level of submaintenance on hay with Groups II and III. Since these metabolism values are referred to uniform body-surface or, more properly, to the general body-mass in its more accurate morphological relations, and thus differences in weight taken into account, the difference between these two average values of 2,150 calories and 1,475 calories speaks for a specific depression in metabolism due to undernutrition. Unquestionably the cell activity is at a greatly lower level. The important fact, however, that the cell function is not damaged by this protracted undernutrition is brought out by the almost explosive resumption of the original metabolic level as a result of even a moderate increase in the amount of feed.

## Energy Relationships.

### THE ENERGY BALANCE DURING UNDERNUTRITION.

Two essentially different methods are in use for estimating whether or no an animal is in energy equilibrium. The first and simplest is the time-honored method of relying upon uniformity of body-weight. If an animal retains a uniform body-weight over a long period, it has been commonly assumed that the adjustment of energy intake is such as to counterbalance exactly the energy output. However, owing to the difficulties of securing accurate records of body-weights (because of the gross influence of variations in drinking-water and particularly because of the inevitable changes in the amount of "fill"), the body-weights of ruminants can at best have but a very uncertain value in accurate scientific computations. The second method is to place the animal inside a respiration chamber and study the actual energy output. Under such conditions, however, the energy production must of course be limited to that during reasonably quiet stall confinement. This latter method has been extensively employed by Kellner, Zuntz, and Armsby in their respiration experiments, in which the animals were confined not only for one day, but frequently for several days, and allowed to stand or lie at leisure, their activity, however, being restricted to that possible when stall-confined.

In practically all of the earlier respiration experiments the increment in heat due to digestive activity, to eating, and to rumination was included and, indeed, it should be, as it is a part of the energy output in the normal life of any steer. Our own respiration experiments were carried out, as has been previously outlined (see p. 197), in an entirely different manner. Our first problem was to study the influence of undernutrition upon the standard metabolism. For this purpose we considered that if under any standard condition the ration had an influence upon metabolism, this influence would be shown as well in a short period under comparable conditions as it would in a 24-hour period, even though the latter would more nearly approximate the daily life of stall-fed animals. Our experiments were therefore made only in short periods, when the steer was standing and had no opportunity for lying down. Moreover, they were made from 24 to 26 hours after the last feed was taken, in order to minimize the increment in heat-production due to digestive activity and rumination. While this experimental procedure suffices perfectly to indicate very clearly indeed, and perhaps more clearly than 24-hour experiments would, the profound influence of the submaintenance ration upon vital processes (as set forth in the foregoing chapter), it fails signally to give us accurate information as to the probable 24-hour requirements of our steers. In the first place, the metabolism in the lying position is measurably less, perhaps 30 per cent less, than in the standing position, and yet our steers were as a rule not studied while lying down. Secondly, the influence of activity was designedly minimized, for only periods indicating complete or approximately complete muscular repose were used by us, and in many periods when great activity took place measurements were carefully avoided. In the third place, no feed was given during the period inside the respiration chamber, thus ruling out the measurement of the metabolism during eating and rumination. Finally, it should also be pointed out that our method of

procedure minimized, although it did not entirely eliminate, the great stimulus to metabolism resulting from the ingestion of feed, a stimulus which, while perhaps not taking place immediately after eating, is very pronounced after a few hours and may reach a very great height within 8 to 10 hours.

### Standard Heat-production as an Index of Probable Total Energy Requirements.

It is important to recognize that all of our so-called "standard" metabolism measurements were made under special conditions and are not directly comparable with the average 24-hour metabolism measurements made by other observers. For their original purpose our measurements are, we believe, preeminently satisfactory. It is a matter of considerable regret to us, however, that the experiments could not have been prolonged, in certain instances at least, to include the measurement of what would correspond to the normal 24-hour heat-production of these animals while on submaintenance hay rations as compared to the normal 24-hour heat-production while subsisting upon a full maintenance ration of hay. Our apparatus was not designed primarily for long experiments. Our staff was limited in numbers; indeed, when compared to the staff ordinarily employed in 24-hour experiments it was pitiably small, and yet in spite of this fact one 24-hour experiment was carried out. Even this experiment, however, is not directly comparable with the earlier work, for the experiment did not begin until the steer had been some 7 hours without feed, although it should be pointed out that the quantity of hay given was but 2,000 grams, i. e., approximately one-half the submaintenance ration.

At the risk of laying perhaps too much emphasis upon this one experiment, we present the data in Table 82, to suggest a possible method of estimating approximately the total 24-hour requirements of our other steers while on feed. This experiment was made with steer A on April 6–7 and continued for 24 hours, the periods being 3 or 4 hours in length. The observations began at $1^h\ 13^m$ p. m., April 6, and ended at $1^h\ 13^m$ p. m., April 7. At $6^h\ 45^m$ a. m. on April 6 the steer ate 2,000 grams of hay. The heat-production was computed from the carbon-dioxide production (reported in Table 57, p. 213), assuming a calorific value of 3.1 calories for each gram of carbon dioxide. The activity throughout practically the entire 24 hours was that usually shown by our steers under the conditions of our experiments, although it is important to note that there was no opportunity for lying down. The experiment began about 7 hours and ended 31 hours after the ingestion of feed. Usually our experiments began 24 to 26 hours after the morning feed. In this particular experiment on April 6–7 steer A received in the morning 2,000 grams of hay. Ordinarily he would not have been put into the respiration chamber until the next morning, or 24 hours after having received 2,000 grams of hay. Consequently, this experiment does include in part the measurement of any stimulus to metabolism produced by approximately one-half of the small daily allotment of hay.

The values for the heat-production per hour are of interest as indicating the possible gradation in heat-production following the ingestion of feed. The total heat-production per 24 hours was 10,600 calories. The heat-production following the seventh hour after feed ingestion steadily decreased, but re-

mained at about 500 calories per hour or 12,000 calories per 24 hours until $9^h\ 13^m$ p. m., i. e., for at least 8 hours. At the end of 31 hours after the last feed it had fallen to 366 calories per hour. This last value corresponds to 8,800 calories per 24 hours and may be taken as representing not far from the standard metabolism usually measured on this animal. For example, the standard metabolism of steer A measured on March 30 was 8,300 calories per 24 hours, on April 13 was 8,200 calories per 24 hours, and on the average from January 19 to May 25 was 8,600 calories per 24 hours. The agreement among these figures is not very far from that normally to be expected, and is a further check upon the relationship between the standard metabolism and that obtaining during periods of greater digestive activity.

TABLE 82.—*The standard heat-production of steer A after the ingestion of 2,000 grams of hay. (April 6–7, 1920.)*

| Period. | Length of period. | Hours after feed. | Heat-production. During period. | Heat-production. Per hour. | Remarks. |
|---|---|---|---|---|---|
| | *hours.* | | *cal.* | *cal.* | Steer A received 2,000 gm. hay at $6^h\ 45^m$ a. m., April 6. He weighed 516 kg. on the morning of April 6 and 508 kg. on the morning of April 7. |
| $1^h 13^m$ p. m. to $5^h 13^m$ p. m. | 4 | 7 to 11 | 2,011 | 503 | |
| 5 13 p. m. 9 13 p. m. | 4 | 11 15 | 1,989 | 497 | |
| 9 13 p. m. 1 13 a. m. | 4 | 15 19 | 1,810 | 453 | |
| 1 13 a. m. 4 15 a. m. | 3 | 19 22 | 1,289 | 430 | |
| 4 15 a. m. 7 13 a. m. | 3 | 22 25 | 1,159 | 386 | |
| 7 13 a. m. 10 13 a. m. | 3 | 25 28 | 1,280 | 427 | Assumed 3.1 calories per gram of carbon dioxide (see Table 57, p. 213). |
| 10 13 a. m. 1 13 p. m. | 3 | 28 31 | 1,097 | 366 | |
| Total | 24 | 7 31 | 10,635 | ..... | The average chamber temperature in the successive periods was 15.7°, 16°, 15°, 15°, 15°, 15.5°, and 16.5° C., respectively. |

If we assume that the value of 10,600 calories, as computed from the carbon-dioxide production, represents the 24-hour requirement of steer A, we find that this is about 2,000 calories per day above the so-called "standard metabolism," but we can not ascribe this increase of 2,000 calories directly to the ingestion of 2,000 grams of hay. A number of factors enter into an interpretation of this increase in metabolism during the feeding period. The 10,600 calories, as measured, include in addition to the standard metabolism an increment due to the effect of 2,000 grams of hay, an amount of feed which was but one-half the usual daily feed at this time. Is the total increment in metabolism proportional to the weight of hay or not? Between the seventh and the eleventh hour after the ingestion of feed the highest heat-production, approximately 500 calories per hour, was noted. It is probable that some increase in metabolism took place before the seventh hour, but this increase was not measured. The actual increase due to the activity of eating was also not measured. On the other hand, during 24 hours the animal would unquestionably, under ordinary conditions, have been lying down for a considerable period of time, and this would correspondingly lower the metabolism. From these data, therefore, one would say that the probable 24-hour metabolism of steer A at this time is not represented by the value of 10,600 calories, but that this figure would have to be increased somewhat to include the rise in metabo-

lism occurring during the first 7 hours after the ingestion of the 2,000 grams of hay, and would have to be decreased because of the lower metabolism during the time occupied by the steer in lying down. The exact apportionment of the corrections to be applied to this value of 10,600 calories is very difficult. Indeed, we probably are not justified in attempting such corrections. Nevertheless, it is of such great importance to try to make some estimate of how far the metabolizable energy in the rations, not only of steers A and B, but likewise of steers 1 to 12, actually met the probable needs of these animals, that further consideration may perhaps be permitted us.

### Metabolizable Energy in Feed and the Probable Energy Requirements.

Before attempting a correction of the standard metabolism measurement to bring it to the probable total 24-hour basis, we believe that an examination of the body-weights of these steers, particularly when referred to the metabolizable energy in feed, will throw considerable light upon the probable total 24-hour heat-output. With Group IV the average metabolizable energy in feed during the long period of undernutrition (periods 2 to 11), was 8,100 calories per day in the case of steer A and 7,900 calories per day in the case of steer B (see Table 41, p. 168). The average standard heat-production per 24 hours of these animals when on the submaintenance level (see Tables 79 and 80) was 8,600 calories with steer A and 9,000 calories with steer B. In both instances, therefore, it is seen that the metabolizable energy in feed was measurably less than the computed standard heat-production. On this basis alone we would expect to find that the animals were not in equilibrium, unless the standard heat-production as computed was actually very much above the probable 24-hour requirements, and our conviction thus far is that the measurement of the standard metabolism must ultimately be corrected by an additive factor due to the cost of digestion and to the actual exercise of eating and by a small subtractive factor due to the difference in metabolism between standing and lying during the period when the animal would normally be lying down.

But from the body-weight curves further evidence can be derived. It has been frequently pointed out that most of the steers toward the end of the period of curtailed rations showed a tendency to reach a plateau in weight, which would imply that the curtailed rations at that time sufficed to prevent further loss. In other words, as the animal grew smaller and the heat-production became less, a point was finally reached where the intake equaled the output and body-weight was maintained essentially constant over a relatively long period. Thus, if we examine the body-weight curves for Group II, we find that steer 1 shows a variation of but 2 kg., covering a period from April 20 to May 5; steer 3 has a practically constant weight from April 20 to May 5; with steer 7 there is a change of hardly 5 kg. from April 6 to May 5; steer 10 shows a change of but 5 kg. between April 13 and May 5; and steer 11 shows a change of but 5 kg. from April 12 to May 5. Of the steers in Group III, steer 6 has seemingly nearly reached a weight level towards the end of the undernutrition period, but his body-weight curve has a slight tendency downwards; steer 8 changes but 3 kg. in weight from April 12 to May 5; steer 9 has lost only 4 kg. from April 13 to May 5; and steer 12 has lost about 8 kg. from April 4 to May 5. The weight curves for these steers, therefore,

indicate in practically all cases constancy in body-weight toward the end of the submaintenance period. In striking contrast to this is the fact that the curves for both steers A and B show no tendency for the body-weight to remain constant, for the slope of the curves in the last few weeks of submaintenance is essentially that throughout the entire period of ration curtailment.

A possible, although we believe hardly probable, explanation of this flattening-out of the weight curves of the animals other than steers A and B at this season of the year is that it is more or less coincidental with a warmer season. It is not inconceivable that with the probable onset of warm weather about the first of April the heat-output decreased, there was a certain degree of

TABLE 83.—*Comparison of the metabolizable energy in feed and the standard heat-production at the low submaintenance level, Groups II, III, and IV.* (*Average values per 24 hours.*[1])

| Group and steer No. | Average body-weight. | Metabolizable energy in feed. | Standard heat-production. | | Metabolizable energy in feed per 500 kg. | |
|---|---|---|---|---|---|---|
| | | | As measured. | Increased by 10 p. ct. | $W$. | $W^{3/4}$. |
| Group II: | *kg.* | *cal.* | *cal.* | *cal.* | *cal.* | *cal.* |
| 1 | 457 | 7,400 | 7,100 | 7,800 | 8,100 | 7,900 |
| 3 | 383 | 7,800 | 7,000 | 7,700 | 10,200 | 9,300 |
| 7 | 352 | 7,000 | 6,200 | 6,800 | 9,900 | 8,800 |
| 10 | 456 | 8,700 | 7,300 | 8,000 | 9,500 | 9,300 |
| 11 | 386 | 7,000 | 6,700 | 7,400 | 9,100 | 8,300 |
| Group III: | | | | | | |
| 6 | 340 | 5,900 | 5,800 | 6,400 | 8,700 | 7,600 |
| 8 | 343 | 6,100 | 7,000 | 7,700 | 8,900 | 7,800 |
| 9 | 453 | 8,000 | 7,400 | 8,100 | 8,800 | 8,500 |
| 12 | 292 | 5,100 | 5,600 | 6,200 | 8,700 | 7,300 |
| Group IV: | | | | | | |
| A | 468 | 7,600 | 8,600 | 9,500 | 8,100 | 7,900 |
| B | 443 | 7,300 | 9,000 | 9,900 | 8,200 | 7,900 |

[1] The values for metabolizable energy in feed are based on the rations given during the last week of submaintenance in the case of Groups II and III and the last 2 weeks in the case of Group IV; those for the standard heat-production are based on measurements secured during the entire period of submaintenance, excluding the period of adjustment at the start in the case of Groups II and III.

muscular relaxation, and hence the energy intake and output automatically more nearly balanced. Still, we must emphasize that thus far throughout our entire report it has been frequently pointed out that the effect of a difference in temperature has almost invariably been such as to suggest that the metabolic level is lower with the lower temperature, although this is quite contrary to all previously existing views with regard to the relationship between the environmental temperature and metabolism.

It is important next to consider how the metabolizable energy supplied to the animals that seemed to indicate weight constancy compared with their measured "standard metabolism." In Table 83, therefore, we have recorded the average metabolizable energy in the feed per day during the last week on submaintenance rations for each of the steers in Groups II and III and during the last 2 weeks for steers A and B, although it should be noted that

the amount of metabolizable energy in the feed was practically constant in every case for many weeks prior to the end of the period of curtailed rations. For comparison with these values we give the average values for the standard metabolism of the steers during the major part of the submaintenance period, omitting the period of adjustment to the low feed-level at the start. These averages are derived from data in Tables 3, 37, 68 to 72, 74 to 77, 79, and 80.

The metabolizable energy was more than sufficient to cover the standard metabolism (as measured) of 7 of the 11 steers, namely, Nos. 1, 3, 7, 10, 11, 6, and 9, but was less than the standard metabolism of steers 8, 12, A and B. On the basis of this comparison between the metabolizable energy in the feed and the standard metabolism it can be seen that if the standard metabolism truly represented the total 24-hour caloric output, those animals that were furnished an amount of metabolizable energy greater than their standard energy output should not only have held their weight, but possibly actually have gained somewhat. Conversely, with those animals whose standard metabolism was measurably higher than the metabolizable energy, one would expect a continuous loss in weight, always providing that the standard metabolism as measured is a true picture of the total 24-hour output. While in the case of steers A and B the body-weight has no tendency to reach a plateau or constancy toward the end of the undernutrition period, thus substantiating fully the indication that the 24-hour heat-output must have been greater than the metabolizable energy, the situation is by no means clear in the case of steers 8 and 12.

An examination of the body-weight curves of these animals shows very small weight changes during the latter part of the undernutrition period. In the case of steer 8, where there is a difference between the metabolizable energy and the standard metabolism of 900 calories, there is seemingly an almost perfect flattening of the body-weight curve during the last 2 weeks of undernutrition, with indeed a slight increase in weight. In the case of steer 12 there is a difference of but 500 calories and practically no change in the body-weight level in the last 2 weeks. Thus, although with steers 8 and 12 the energy intake was respectively 900 and 500 calories less than the energy output, the body-weight curves are not at all in conformity with the general picture of caloric deficiency. The evidence is, in the case of steers A and B, however, definitely indicative that there has been a continuous draft upon body material.

This comparison of the metabolizable energy and the standard metabolism does not take into consideration in any sense differences in size of the animals, and the question naturally arises as to how the metabolizable energy in the feed of these steers compared per unit of weight or per unit of surface-area. For this comparison we have reported in the last two columns of Table 83 the average daily metabolizable energy in feed referred to 500 kg. of body-weight and likewise referred to the two-thirds[a] power of 500 kg., the time represented being, as stated before, the last week of undernutrition in the case of Groups II and III and the last 2 weeks in the case of Group IV.

[a] Possibly reference to the five-eighths power would have been more in accordance with probable facts.

Considering, first, the metabolizable energy per 500 kg. of body-weight, we note that steers A and B were furnished a lower amount of metabolizable energy than any of the other animals save steer 1. Steers 6 and 12 had the next lowest amount of metabolizable energy per 500 kg. of body-weight, and, as already pointed out, the amount furnished steer 12 was slightly deficient when compared to his standard metabolism. Steer 8, with which was noted the greatest discrepancy (other than with steers A and B) between the metabolizable energy and the standard metabolism, i. e., 900 calories, received a somewhat higher amount of metabolizable energy per 500 kg. than 4 of the other steers in Groups II and III. It seems quite clear, however, that steers A and B received on the whole a low amount of metabolizable energy per 500 kg. of body-weight. This picture for steers A and B is not so sharply defined, however, on the basis of the two-thirds power of 500 kg. of body-weight. Here we find that these two steers received an amount of metabolizable energy fully as high as and indeed higher than that received by 4 of the other steers in Groups II and III. The lowest amount, on this basis, is noted with steer 12 and the next lowest with steer 6. From a general inspection of the data in Table 83 it would appear that steers 3, 7, 10, and 9 were perhaps most liberally provided with metabolizable energy, both on the basis of equal weight and equal surface-area (in so far as the two-thirds power of the weight implies surface-area), and it is important to note that in the case of these steers the total amount of metabolizable energy consumed was appreciably above their measured standard metabolism.

From the picture of the plus and minus differences shown by the comparison of data in Table 83, the inference seems reasonably well founded that the standard metabolism, as measured, represents not far from the true 24-hour energy requirements, although probably the values should be raised somewhat. The exact amount of this additive correction remains and always will remain unknown. Still, if we assume that the standard metabolism indicates not far from the 24-hour requirements, we may more carefully consider in detail how nearly the metabolizable energy in the various rations met the needs of the body and to what extent the body material had been drawn upon during the prolonged period of undernutrition.

With steers A and B the steep slope of the body-weight curves toward the end of the submaintenance period, the fact that the metabolizable energy was considerably lower than the standard metabolism, and that the metabolizable energy per 500 kg. of body-weight was low compared with that for the other steers subjected to ration curtailment, furnish strong proof that their so-called "maintenance ration" (upon which the cut was originally made), was probably already somewhat below maintenance. This finding is further substantiated by the fact that both steers during the first so-called "maintenance period" lost about 23 grams of nitrogen per day from the body. Therefore, since with steers A and B the metabolizable energy was not sufficient to meet the body requirements (for it was considerably below the measured standard metabolism and there was a continuous loss in body-weight during the entire period), it would be futile to make a direct comparison of the metabolizable energy and the energy output and expect that there would be a balance.

It is important to point out the need for caution in assuming that when body-weight is maintained at a uniform level there is simultaneously an energy balance. For example, from April 13 to May 5, and indeed for a few days after May 5, the body-weight of steer 10 remained practically constant. Is it not justifiable to compare the metabolizable energy provided in the feed with the standard metabolism at this time and expect a balance? The metabolizable energy furnished steer 10 for the last week of submaintenance, April 28 to May 5, was 9,500 calories per 500 kg. of body-weight. At or about this time he showed a standard metabolism of not far from 8,000 calories per 500 kg. In other words, he was given metabolizable energy amounting to 9,500 calories and his heat-production was 8,000 calories. On this basis alone he should not have been in weight equilibrium. He should actually have been gaining in weight, for he had seemingly 1,500 calories above his needs. Now, in this consideration the value of 9,500 calories is based upon several weeks of almost constant rationing, and the value of 8,000 calories upon two standard metabolism measurements on May 3 and May 8, respectively, which agreed perfectly. In fact, the standard heat-production per 500 kg. of body-weight was 8,100 calories on the average for the entire period of undernutrition. The body-weight curve shows unusual uniformity for almost a month, with certainly no tendency to rise noticeably, suggesting the addition of tissue or flesh. This illustration would seem almost to preclude any comparison of the metabolizable energy and the standard metabolism. We think the comparison is permissible, however, provided too great a refinement is not attempted and provided the variability between the different animals is thoroughly recognized.

The importance of the comparison is not to note the individual energy balances for the last week or two weeks of the curtailment of ration, but to note in how far the standard metabolism may be taken as a measure of the 24-hour heat-output. The metabolizable energy is known with a reasonable degree of accuracy. The standard metabolism is likewise known with an approximate degree of accuracy. The actual 24-hour heat-output is not known, but must be estimated. We believe it is somewhat higher than the average measured standard metabolism. As a very general, conservative figure (for seemingly some figure would furnish helpful estimates), we suggest that the "standard" metabolism increased by 10 per cent would represent the total 24-hour output on the average. On this basis we note from the data in Table 83 that the probable 24-hour heat-output is greater than the available metabolizable energy in the case of steers 1, 11, 6, 9, and 12, and very much greater in the case of steers 8, A, and B, that is, 8 out of the 11 animals have a probable 24-hour heat-output measurably greater than the metabolizable energy. But with 3 steers, Nos. 3, 7, and 10, the metabolizable energy is slightly greater than the probable 24-hour heat-output during the last week of the undernutrition period. Numerically these conclusions are justified. Practically, it can be seen that under these conditions Nos. 3, 7, and 9 are really in energy equilibrium, leaving No. 10 alone of all the animals showing an apparent plus of metabolizable energy over the standard metabolism increased by 10 per cent. In this comparison undoubtedly too great a degree of refinement has been attempted, and if we consider the major differences, we find that only in the cases of steers 8, 12, A, and B are there very pro-

nounced deficiencies in metabolizable energy as compared to the estimated 24-hour requirements, the other steers showing essential uniformity or a balance.

At this point it is important to note that the increment of 10 per cent very arbitrarily assigned to the standard metabolism measurement to represent, if possible, the 24-hour requirements, is based upon an analysis of the figures obtained during the last week or two of the undernutrition period. We are by no means certain that an additive correction of 10 per cent would hold during the earlier part, particularly the transition phase of the undernutrition period. Indeed, it is not improbable that the 24-hour heat-output is more than 10 per cent above the measured standard metabolism at the earlier stages. That the correction should be 15 per cent or 20 per cent we can not state. It is important, however, to make at least tentative computations upon the basis that the standard metabolism is to be increased only by this suggested factor of 10 per cent and to compare the total computed caloric output with the metabolizable energy. This has been done in the following manner with the steers subjected to ration curtailment:

Groups II and III were subjected to curtailed rations for 135 days and Group IV for 140 days. The total metabolizable energy for the entire period of 135 and 140 days, respectively, has been computed for each steer (based upon the average metabolizable energy per day as given in Tables 41 to 44) and recorded in column *a* of Table 84. The total standard heat-production (recorded in column *c*) was obtained for all steers by multiplying the average daily heat-production (as recorded in Tables 68 to 80),[a] measured over the *entire* period by the total number of days. For the sake of clearness the results are expressed in Table 84 not in terms of calories but using the term introduced by Professor Armsby, the "therm," i. e., 1 therm is the equivalent of 1,000 large calories. It is important to note that the use of the general average value obtained during the entire period of undernutrition may be subject to the criticism that in many instances the measurements of metabolism were not equally distributed throughout the entire 135 or 140 days. In many cases a somewhat larger number of measurements were made at the start, particularly during the period of transition, when the standard metabolism had not been so profoundly affected by the curtailment of ration. Under these conditions the average value is naturally somewhat too high. It did not seem justifiable, however, to attempt to refine the computations by interpolating for each day. But if this criticism holds, as we think it does, the total standard metabolism as computed is a little higher than would be found were the true average value used.

As a result of the careful analysis of the data for the metabolizable energy, the standard metabolism, and the analysis of the weight curves for the last one or two weeks (see Table 83, p. 309) we have assumed that the probable 24-hour heat-production would be better expressed by the standard metabolism measurement increased by 10 per cent rather than by the standard metabolism measurement itself. Accordingly, we have applied this correction to the values in column *c* of Table 84 and recorded the new values in column *d*.

[a] The average daily heat-production for the *entire* submaintenance period is not given in Tables 74 to 77 for the steers in Group III, but two averages for the two different submaintenance levels, and we had to make a new average for the entire period for use in Table 84.

It now remains to compare the total metabolizable energy with this tentatively corrected total standard heat-production, as has been done in the last column (*e*) of the table. Here the singular fact is brought out that with steers 10, 6, and 9 the total metabolizable energy was apparently somewhat greater than the computed total heat-production, which might lead to the conclusion that there could have been no loss in weight with these animals throughout this period other than possibly a change in fill, at least no loss in weight of organized tissue. But an examination of the body-weight curves for these 3 steers shows without doubt that there must have been a consider-

TABLE 84.—*Comparison of the total amount of metabolizable energy in feed and the total standard heat-production during the entire period of undernutrition, Groups II, III, and IV.*

| Group and steer No. | Average body-weight during undernutrition. | Metabolizable energy in feed.[1] | | Standard heat production. | | (*e*) Surplus or deficit of metabolizable energy. (*d*−*a*) |
|---|---|---|---|---|---|---|
| | | (*a*) Total. | (*b*) Per 500 kg. | (*c*) Total.[2] | (*d*) Total increased by 10 p. ct. | |
| Group II: | *kg.* | *therms.*[3] | *therms.* | *therms.* | *therms.* | *therms.* |
| 1 | 493 | 1,145.4 | 1,161.7 | 1,134.0 | 1,247.4 | −102.0 |
| 3 | 418 | 1,063.2 | 1,271.8 | 1,066.5 | 1,173.2 | −110.0 |
| 7 | 381 | 952.2 | 1,249.6 | 985.5 | 1,084.1 | −131.9 |
| 10 | 492 | 1,184.1 | 1,203.4 | 1,053.0 | 1,158.3 | + 25.8 |
| 11 | 424 | 958.8 | 1,130.7 | 1,066.5 | 1,173.2 | −214.4 |
| Average | | | 1,203.4 | | | |
| Group III: | | | | | | |
| 6 | 375 | 1,007.7 | 1,343.6 | 891.0 | 980.1 | + 27.6 |
| 8 | 384 | 1,039.5 | 1,353.5 | 1,026.0 | 1,128.6 | − 89.1 |
| 9 | 498 | 1,272.0 | 1,277.1 | 1,080.0 | 1,188.0 | + 84.0 |
| 12 | 330 | 888.3 | 1,345.9 | 850.5 | 935.6 | − 47.3 |
| Average | | | 1,330.0 | | | |
| Group IV: | | | | | | |
| A | 522 | 1,134.0 | 1,086.2 | 1,204.0 | 1,324.4 | −190.4 |
| B | 495 | 1,106.0 | 1,117.2 | 1,260.0 | 1,386.0 | −280.0 |
| Average | | | 1,101.7 | | | |

[1] Computed from data in Tables 41 to 44 (pp. 168 to 171), by multiplying the average metabolizable energy per day by the number of days represented in the period.

[2] Computed by multiplying the average standard 24-hour heat-production during the *entire* submaintenance period by the total number of days represented, i. e., 135 or 140 days.

[3] For the sake of brevity, the values are expressed not as calories but as therms (1 therm is equivalent to 1,000 large calories).

able loss of tissue, fat, and flesh. No nitrogen-metabolism experiments were made with them, and hence no positive evidence of protein-loss is at hand, although such a loss is highly probable. Under these conditions it is obvious that this method of computation in Table 84 is not justifiable, although large deficiencies in the amount of metabolizable energy available are noted with steers 11, A, and B; in fact, deficiencies of 89 therms or more are noted with steers 1, 3, 7, 11, 8, A, and B.

It is perhaps worthy of record that the 4 animals in Group III, if averaged as a group, would show practically no deficit while all the animals in Group II except No. 10 show a large deficit of metabolizable energy. It will be recalled that Group II was subjected to a curtailment of ration amounting to somewhat

more than 50 per cent of maintenance and that Group III was subjected, first, to a curtailment of but about 40 per cent and subsequently to a curtailment of approximately 60 per cent of maintenance. Hence, it would seem as if the total metabolizable energy would be less for the steers in Group III than for those in Group II. Before drawing this conclusion, however, it is important to compute the metabolizable energy for each steer upon the basis of equal body-weight, for example, upon the basis of 500 kg. of body-weight. These computations, which are given in column *b* of Table 84, bring out the singular fact that on the average Group III had the highest total amount of metabolizable energy per 500 kg. of body-weight, Group II had approximately 10 per cent less than Group III, and Group IV had approximately 8 per cent less than Group II. On this basis, therefore, one would expect to find the steers in Group III nearest to energy equilibrium (as indeed they seemingly are, according to Table 84), those in Group II next nearest to energy equilibrium, and those in Group IV the farthest from energy equilibrium. By these crude tests, therefore, these three groups fall into quite a proper series.

Although Group III as a whole shows practical equilibrium on this basis of computation, the data obviously can not represent a true energy balance, for throughout this period of undernutrition there was a total loss in weight of 92 kg. with steer 6, of 130 kg. with steer 8, of 111 kg. with steer 9, and of 110 kg. with steer 12, or 111 kg. on the average. The amount of fill in these large ruminants is known only with a certain degree of approximation, but might be represented on the average by a rough, tentative figure of 70 kg. It is clear that there must be a certain amount of fill remaining in these animals even at the end of the submaintenance period. No estimate of this amount has been made or can be made, we believe, unless one could subject these steers at the end of such a long period of curtailment of ration to a short fasting experiment and note the curve of decrease of fecal excretion as time goes on. Let us assume, however, that there would be at least 25 kg. of fill (we believe it probably would be more) remaining in the intestinal tract at the end of the submaintenance period. On the basis that there were 70 kg. at the start, there would thus be a maximum withdrawal of 45 kg. from the fill. But the total loss in weight of these animals in Group III was, as we have seen, 111 kg. on the average. Under the circumstances it is obvious that Group III could not have been in energy equilibrium, and it is highly probable that the tentative, additive correction of 10 per cent to the standard metabolism to represent the probable 24-hour requirements is too small.

Whatever considerations apply in the case of Group III to the comparison of the total metabolizable energy and the total heat-production (as computed from the standard heat-production increased by 10 per cent) apply with even greater force to Groups II and IV, for if we admit that the figures in column *d* of Table 84 do not properly represent the total heat-production of the steers in Group III and that they are obviously too low, the same reasoning must apply to similar values for Groups II and IV, i. e., that they are too low, and yet we find in column *e* on the whole large deficits in metabolizable energy for these groups. Any further correction, therefore, of the standard metabolism would tend to increase these caloric deficits. It was hoped, particularly with steers A and B, that, knowing the nitrogen loss and the loss in protein and flesh computed therefrom, together with the calories

represented in the protein lost, we might be able to compute tentatively the calories lost in fat, thereby obtaining indirectly a measure of the actual amount of fat and flesh lost by these steers during the 140 days of undernutrition. The whole method of computation hinges, however, upon the additive correction to be applied to the standard metabolism measurement to bring it to the probable 24-hour requirements. Frankly, we see no definite evidence as to the magnitude of this correction. Undeniably the animals lost a certain proportion of fill. It is absolutely proved that steers A and B lost large amounts of nitrogenous tissue. As a matter of fact, from the data in Tables 34 and 35 it can be seen that steer A lost during periods 2 to 11 a total of 1,262 grams of nitrogen, corresponding to 30.3 kg. of flesh, computed in the usual manner. Similarly, steer B lost 1,384 grams of nitrogen, corresponding to 33.2 kg. of flesh. Assuming a maximum withdrawal of fill of 45 kg. and adding thereto the approximate amount of 32 kg. lost on the average in the form of flesh, we have accounted for 77 kg. of the loss in body-weight. With steers A and B, however, the total loss in body-weight throughout this period was 132 and 125 kg., respectively. To attribute the entire difference between 77 kg. and 132 or 125 kg. to fat is probably very questionable, and yet we are forced to this tentative computation for lack of other positive data.

On this basis steers A and B lost approximately 52 kg. of fat on the average throughout the 140 days, or approximately 370 grams of fat per day. The energy from this amount of fat would correspond to about 3,300 calories per day, which represents a real deficit. The caloric loss through protein must also not be neglected. Both steers lost on the average approximately 1,300 grams of nitrogen in 140 days, or about 9 grams per day, and the net energy lost in this amount of protein would correspond to approximately 225 calories per day. There would be, therefore, a total deficit of 225 plus 3,300 calories, or approximately 3,525 calories per day, and in 140 days a sum total of 493,500 calories. By the method of computation in Table 84, the deficit between the total metabolizable energy and the total heat production computed from the standard metabolism is on the average but 235,200 calories, while the foregoing computation from the assumed loss of fat points towards a much greater loss of heat from the body. At the end of the submaintenance period, therefore, with steers A and B there was a deficit of approximately 1,300 grams of nitrogen and, as computed above, approximately 52 kg. of fat which must be charged up to the cost of maintaining these steers on a very low level for 140 days.

To attempt to apply these computed losses to the probable losses of the other steers brings in the numerous problematical, indeed questionable, factors already pointed out. Undoubtedly the other animals also lost nitrogen, although probably not quite so much as steers A and B, for we believe that their supply of metabolizable energy was a little more liberal than was that of steers A and B. Undoubtedly they underwent a fat-loss, again probably not so great as with steers A and B. But if we accept the data secured with steers A and B, we find that as a result of 140 days of undernutrition adult steers as a whole may be carried through the winter on scant hay rations, but at the expense of a loss of 1,300 grams of nitrogen and 52 kg. of fat. Figures for the actual losses of protein are, of course, only to be obtained by continuous nitrogen-metabolism experiments such as were made

with steers A and B. The results for these 2 animals are most satisfactory, and we have every confidence in them. The important element from the energy standpoint, however, is the probable loss of fat. The admittedly very tentative computations outlined in this section could only be verified by a series of metabolism measurements in which the animals would be studied not only once a week, and under our so-called "standard" conditions, but more frequently and, indeed, in 24-hour periods. We do believe, however, that from the practical standpoint our estimates of the cost to the adult body of subsisting upon this scant ration (i. e., approximately 50 per cent of hay maintenance) for 140 days, namely, the loss of 1,300 grams of nitrogen and the loss of 52 kg. of fat, probably represent fairly accurate average figures.

To have maintained these steers throughout this period without loss of either protein or fat would have called for more than double the amount of hay and probably, judged from the experience of Armsby and from our own experience with steers A and B, the regular addition of some nitrogenous concentrate. In any consideration of the economic phase of this study, therefore, it would be necessary to recognize that our so-called "maintenance" periods were really not maintenance but were already somewhat submaintenance, and that to insure that the steers would come through the winter without further loss of protein or fat, at least the amount of hay given them in our maintenance periods should be supplied, probably somewhat more, and in all probability 300 or 400 grams of concentrates per day. For this particular phase of the problem we feel that special economic treatment is necessary. The absence of 24-hour experiments, the sparsity of metabolism experiments throughout the year, and particularly the great economic disadvantages under which we labored in purchasing and selling our steers, paying extremely high rates for them as well as for the hay and grain used, and being forced by the experimental program to sell them at a very low price, make the economic consideration quite out of place in this report.

### THE ENERGY DURING REALIMENTATION.

Physiologically one of the most important points to be considered in connection with this research is as to the effect of the long period of undernutrition upon the capacity of the animal subsequently, with plenty of feed, to regain its initial weight and to fatten, when given fattening rations. From the experience of wild animals it is hardly to be supposed that any serious, permanent detriment could be caused by a relatively long period of undernutrition. We adjusted our experimental series in order to accumulate evidence with regard to exactly this point, and a certain amount of discussion should be accorded this subject here, although the economic phase of the question may more properly be left for consideration elsewhere.

At the end of the period of submaintenance practically all of these steers had fallen off very considerably in body-weight. Even the 3 controls had lost slightly upon the ration exclusively of hay. The other steers had lost somewhat over 100 kg. on the average. In refeeding it was therefore necessary, first, to replace this lost material, noting the amount of feed required and the length of time required to do this. The steers were then to be fattened on a heavy grain ration, to prepare them for final slaughter in the market. The metabolizable energy of the feed throughout all of this time is

known, we believe, with considerable accuracy, and we are therefore able to compute the metabolizable energy required for the total gain in weight made by the different steers. Of the innumerable methods of computation and subdivisions of the feeding periods (such as the time required and the metabolizable energy necessary to regain the initial weight, and the relationship between the feed consumed and the final addition of fat or flesh) we have chosen as the simplest, and perhaps at this point the only permissible one, the computation of the metabolizable energy required to bring these steers from their lowest weight level, i. e., on May 5, to a condition fattened for market. In Table 85 are recorded the total weight gained after the lowest level on May 5, the number of days required to gain this weight, the total metabolizable energy supplied in this length of time, and the metabolizable

TABLE 85.—*Metabolizable energy in feed per kilogram of body-weight gained, Groups I, II, and III.*

| Group and steer No. | Days. | Weight gained after May 5. | | Metabolizable energy supplied during period of gain in weight. | | |
|---|---|---|---|---|---|---|
| | | Total. | Total less 45 kg. (assumed change in fill). | Total. | Per kg. of weight gained. | Per kg. of weight gained corrected for change in fill. |
| Group I: | | *kg.* | *kg.* | *therms.* | *therms.* | *therms.* |
| 4 | 114 | 131 | ..... | 3,565.8 | 27.2 | ..... |
| 5 | 114 | 134 | ..... | 3,935.8 | 29.4 | ..... |
| Group II: | | | | | | |
| 1 | 161 | 230 | 185 | 5,289.2 | 23.0 | 28.6 |
| 3 | 182 | 232 | 187 | 6,538.0 | 28.2 | 35.0 |
| 7 | 161 | 229 | 184 | 4,505.9 | 19.7 | 24.5 |
| 10 | 182 | 241 | 196 | 5,765.2 | 23.9 | 29.4 |
| 11 | 182 | 239 | 194 | 5,553.1 | 23.2 | 28.6 |
| Group III: | | | | | | |
| 8 | 143 | 215 | 170 | 4,386.3 | 20.4 | 25.8 |
| 12 | 182 | 221 | 176 | 4,755.1 | 21.5 | 27.0 |

energy per kilogram of weight gained, the energy figures being given as therms.

In this tabulation of the results it is important to note that with steers 4 and 5 the total weight gained in the fattening period is only about one-half that of the other steers, since they had not undergone the previous large loss in weight. Likewise, the total number of days to gain this weight is much less than with the other steers. We have not incorporated in this table any values for steers 2, 6, and 9, which were brought to market condition on pasture alone, although as a matter of fact a small amount of grain was given to steers 6 and 9 the last few days. Before the steers in Groups II and III were slaughtered they had gained on the average 230 kg. over their lowest level, requiring in general not far from 170 days for this gain. The metabolizable energy supplied for every kilogram of body-weight gained was highest with steers 4, 5, and 3, namely, 27.2, 29.4, and 28.2 therms, respectively. With all the other animals the amounts are somewhat lower, 24 therms or under.

Before making a direct comparison, however, of this cost in metabolizable energy per kilogram of body-weight gained, it is important to note that of the total weight gained in each case a very different value may properly be ascribed to that gained by steers 4 and 5, which started in good condition, and that gained by the other steers, which started from a low level. We have every reason to believe that there was a large increase in the amount of fill with the steers in Groups II and III. The total increase in body-weight does not, therefore, necessarily represent formation of flesh and fat, to which the metabolizable energy would contribute extensively, but a certain portion of it represents inert fill which is rather rapidly acquired, and hence for purposes of comparison a correction should be made for the probable gain in fill. This gain in fill has been estimated to be on the average 45 kg., and accordingly in Table 85 the total weight gained has been corrected for a change in fill of 45 kg. in the case of Groups II and III. Finally, in the last column of the table we have recorded for these two groups the metabolizable energy per kilogram of body-weight gained, corrected for change in fill. These values on the average more nearly approach those found for steers 4 and 5 (uncorrected for fill). It is still highly probable, however, that there were slight changes in the fill of steers 4 and 5, for they lost somewhat in weight throughout the winter, and a part of this loss was undoubtedly in the nature of fill. If any correction for gain in fill is made in the case of steers 4 and 5, the metabolizable energy per kilogram of weight gained by these 2 animals would be increased.

The figures indicate very clearly, however, that the actual cost in metabolizable energy for each kilogram of weight gained, after making correction for the change in fill, is essentially the same with the steers of Groups II and III as is the uncorrected cost for steers 4 and 5. From this evidence alone it is apparent that the undernourished steers did not sacrifice in any way their ability to lay on flesh and that the cost in metabolizable energy in their case was no greater than in the case of the control steers which were put through the fattening process. In this respect, therefore, we have further evidence that the steers in Groups II and III in all probability went to the slaughter house with all of their physiological functions in perfectly normal condition, with the necessary fat for sale deposited, and deposited with an expenditure of metabolizable energy per kilogram of weight gained not essentially different from that noted with the 2 steers which had not been subjected to the rigorous submaintenance régime.

The lack of any satisfactory means of computing the metabolizable energy available to the steers on pasture makes the consideration of steers 2, 6, and 9 wholly impossible. It has already been pointed out that these steers regained their lost weight very rapidly when turned out to pasture, steer 6 regaining his weight in 38 days and steer 9 in 41 days, while the other steers required from 71 to 82 days, save in the special case of steer 10, which was maintained on a hay ration alone for some time and required 115 days. In other words, the pasture steers, Nos. 6 and 9, regained their initial weight in almost one-half the time required by the other steers. As has been pointed out elsewhere (see p. 100), in all probability this gain in weight was by no means solid, substantial flesh, but represented in large part fill and, indeed, a more than normal proportion of fill. The character of this increase in weight was

evident at once in the slaughter tests of these animals, and it is to these tests that we should refer for a more careful comparison of the grass-fed steers with the steers given concentrates.

Here again, it is extremely unfortunate that the exigencies of experimentation demanded, in the first place, that steers 2, 4, and 5 should be slaughtered under entirely different conditions and at a different market than the steers in Groups II and III. Nevertheless, it is significant that in both instances the carcasses of the grass-fed steers were ascribed an altogether different market value and scored entirely different from the carcasses of the steers which were fattened on concentrates. We had hoped to be able to compare accurately the grass-fed steer No. 2 with the grass-fed submaintenance steers, Nos. 6 and 9. This it is almost impossible to do, save on the general basis of the scoring of the animals prior to slaughter and the comments on the character of the dressed beef. In general, no gross difference between Nos. 2, 6, and 9 could be ascribed to the fact that the two latter animals had been subjected to a previous curtailment in ration. They apparently regained their lost weight and were able to get in as good condition on grass alone as was the control steer, No. 2, a fact which again substantiates our general conclusion that the long period of submaintenance rations was not detrimental to the subsequent realimentation of these steers.

The salient and most important feature of the entire investigation, to our mind, is the fact that adult steers may be carried through the winter on extraordinarily low rations, resulting in heavy losses in weight, and yet experience no permanent damage and no disability to resume original weight or, indeed, to gain weight when subsequently given plenty of feed. In this finding the steers duplicated almost exactly the experience of the Nutrition Laboratory in connection with the prolonged undernutrition experiments with humans, where the relative loss in weight was not so great as with these steers, to be sure, but material (10 per cent or more), and on the resumption of full feeding body-weight was rapidly regained and full strength and vigor secured without any untoward results.[a]

## FINAL CONDITION OF STEERS AND THE SLAUGHTER TESTS.

While it was found that the steers that had been upon the prolonged submaintenance rations could not only regain their lost weight with liberal provision of feed, but take on subsequent weight and be fattened or "finished" for market, a more detailed consideration of their final condition and of certain data with regard to the slaughter tests is important before final conclusions are drawn as to the effect of the prolonged submaintenance rations. The slaughtering of the 14 steers unfortunately had to take place at three different times and under three essentially different conditions. Steers 2, 4, and 5, the control animals in Group I, were ready for market considerably before the other steers, and hence it was necessary to slaughter them first. With the idea that probably the larger number of the animals would have to be sent to the same slaughtering establishment such as, for example, Brighton, Massachusetts, special provisions were made to have an expert from the Brighton yard come to Durham and there supervise the slaughtering of the 3 control

[a]Benedict, Miles, Roth, and Smith, Carnegie Inst. Wash. Pub. No. 280, 1919.

animals. The animals in Groups II and III were sent later in the year to Brighton for slaughter, but with the disadvantageous conditions obtaining at the time these two groups were slaughtered, it was decided that slaughtering at Durham was preferable. Consequently steers A and B (a year later) were slaughtered at Durham, but by the local butcher rather than by a professional Brighton beef-dresser. As already outlined, the market conditions had fluctuated very considerably during this time, so that at best our comparisons are complicated.

With steers 2, 4, and 5 no particular difficulty was experienced and the data regarding their slaughter are adequate and satisfactory. Unfortunately, at the time when Groups II and III were shipped to Brighton, a strike was in effect among the employees of the Brighton stockyards. On the day when our steers in these groups were slaughtered an emergency crew of about one-half the normal number necessary for the proper management of the yard had arrived from Chicago and had started dressing beef. Because of the large amount of live stock that had accumulated there was some confusion and the force was naturally working at high pressure. Consequently it was impossible to obtain from the beef-dressers a great deal of cooperation to secure information which it would have been desirable to have in addition to that actually obtained.

The last feed before shipment was given to Groups II and III at 7 a. m., November 6, 1919. They were loaded on the cars at 4 p. m., of the same date and left Durham that evening for Brighton. They were slaughtered between 9 a. m. and 12 m., November 10. No information could be obtained regarding their treatment after arrival in Brighton (some time on November 7) until slaughtered. The feeding was probably very poor and the shrinkage very heavy, since the general appearance of the steers as they entered the slaughtering-pens gave that impression very decidedly.

### Comparison of Condition before Slaughter.

Prior to being slaughtered, all of the steers were scored as to their condition, particularly with regard to their so-called "condition of flesh." For all of the animals except Nos. 2, 4, and 5, this scoring was done by one of us (E. G. R.). The scoring of Group I represents the judgment of the professional beef-dresser from the Brighton market, who superintended the dressing in Durham. It is important to bear in mind that this judgment is quite separate from the consideration of the dressed carcasses, which of themselves demand special inspection. On August 28, 1919, just prior to slaughter, Group I was judged on the live basis as to their general condition of flesh and fat or fitness for slaughter, the result being in abstract, as follows:

*Steer 4.*—General condition very good, smooth, not lumpy, well finished. The value at Brighton on August 28 would be about 13½ cents per pound on the hoof. The animal is good enough, but would take on a Christmas finish; is more like a western steer.

*Steer 5.*—General condition very good, but not so even and smooth as No. 4, although he will bring as much as No. 4 at Brighton. Coarser but fully as fat as No. 4. Is fat enough now and will get lumpy on more feeding.

*Steer 2.*—General condition only fair. The animal is just covered with flesh, but will shrink more than 4 or 5 per cent. Worth about 12 cents at Brighton. In this

connection it may be added that steer 2 was the grass-fed animal of Group I and that the difference in price between 13½ cents for steers 4 and 5 and 12 cents for steer 2 shows the inferiority of this grass-fed animal.

Later in the fall, Groups II and III were judged relative to condition of fatness prior to shipment. Reference is also made to condition of skin and hair, which is generally acknowledged to be a fair mirror of the progress of the laying-on of fat, quite irrespective of the inherent depth of flesh which an animal may be able to develop in different parts of the body.

*Steer 1.*—Skin thick and fairly soft, hair somewhat coarse but glossy. Condition of flesh: fair over ribs, poor over loin and hips; rump and thighs not well fleshed. A poor beef type, as he will dress out with a heavy percentage of bone.

*Steer 3.*—Skin thin and soft; hair soft and glossy. Condition of flesh: on ribs good; loin very good; rump fair but somewhat patchy or lumpy; thighs fairly good. A fairly good beef type.

*Steer 6.*—Skin tight on body; hair somewhat coarse or rough, slightly glossy. Condition: a fair beef type, but lacking in flesh and unfinished for market.

*Steer 7.*—Skin soft, fairly thick; hair soft and glossy. Condition of flesh: ribs well covered; the back well covered forward but not deep over the loin; rump fair, deep and smooth; thighs good. In general a good beef type.

*Steer 8.*—Skin thick and mellow; hair soft and glossy. Condition of flesh: ribs fairly well covered; back well covered on crops and loin; smooth over the rump; thigh fairly well filled. Fair beef type; rather undersized for his age.

*Steer 9.*—Skin thick and fairly tight; hair coarse and harsh. Very poor in flesh. Very poor beef type; will dress out an excess of bone.

*Steer 10.*—Skin thick and soft; hair smooth and glossy. Condition of flesh: on ribs fair but uneven; on back fair on the crops, good on the rump; loin smooth, not very deeply covered; thigh well muscled, deep, and broad. Good beef type.

*Steer 11.*—Skin thick and mellow; hair soft and glossy. Condition of flesh: ribs well covered; back well covered over crops and shoulder; only fair over loin and rump; light in the thighs. Good beef type.

*Steer 12.*—Skin tight; hair slightly harsh. Condition of flesh: ribs poorly covered; crops good; loin fairly thick; rump poor; thighs flat. Poor beef type.

*Steers A and B.*—Neither is in a high state of flesh. Steer A is naturally somewhat better fleshed than steer B, but neither animal is in a finished fat state. Both are, however, in good, vigorous, thrifty condition, as indicated by the general appearance and handling of skin, which is soft and pliable, but lacking the mellowness given by abundant deposition of fat. Both animals would have to be fed at least 2 more months and on heavier grain rations to be classed as "fat" steers.

*General conclusions as to live judgments on grass-fed group.*—Steers 2, 6, and 9, the grass-fed animals, were all in a materially poorer condition of flesh at the time of slaughter. Unfortunately, No. 9 can not be compared with the other 2 animals of this group, due to the fact that he was so unlike in age and conformation. He was especially inferior in the latter respect, which, combined with his age, made him an exceedingly poor beef type in a class by himself, much inferior to either No. 2 or No. 6. There is little obvious difference, however, between No. 2, the control animal fed on grass, and No. 6, the submaintenance animal subsequently brought to condition on grass.

### Comparison of Percentages of Dressed Carcass.

While certain minor parts of the animal, such as the liver, heart, lungs, and hide, are sold after slaughter, the item of greatest importance is the amount of dressed beef (the two sides). As a rough comparison of the state of nutrition of these steers, we have drawn off in Table 86 data regarding the live body-weight, the weight of the dressed sides, and, when known, the amount of free fat, as well as the percentage of dressed beef. The fat was weighed individually only in the case of the steers in Groups I and IV.

Table 86.—*Amounts of dressed beef.*

[The live weights are averages of daily weights for one week just before slaughter.]

| Group and steer No. | Live weight. | Dressed sides. | Fat. | Per cent of dressed beef. |
|---|---|---|---|---|
| High protein: | *kg.* | *kg.* | *kg.* | |
| Steer No. 3.. | 615 | 333 | ..... | 54.1 |
| Steer No. 4.. | 626 | 350 | 28.6 | 55.9 |
| Steer No. 8.. | 572 | 304 | ..... | 53.1 |
| Steer No. 10.. | 697 | 379 | ..... | 54.4 |
| Steer No. 12.. | 513 | 268 | ..... | 52.2 |
| Steer No. B.. | 666 | 381 | 14.6 | 57.2 |
| Low protein: | | | | |
| Steer No. 1.. | 691 | 383 | ..... | 55.4 |
| Steer No. 5.. | 722 | 416 | 34.9 | 57.6 |
| Steer No. 7.. | 579 | 320 | ..... | 55.3 |
| Steer No. 11.. | 625 | 347 | ..... | 55.5 |
| Steer No. A.. | 686 | 402 | 17.6 | 58.6 |
| Grass-fed: | | | | |
| Steer No. 2.. | 518 | 260 | 13.6 | 50.2 |
| Steer No. 6.. | 481 | 247 | ..... | 51.4 |
| Steer No. 9.. | 612 | 272 | ..... | 44.4 |

The percentage of dressed beef ranges from as low as 44.1 per cent with steer 9 to as high as 58.6 per cent with steer A. As a matter of fact, the lowest percentage of dressed beef is found with the three grass-fed animals, Nos. 2, 6, and 9, the latter animal showing a very much lower percentage than either of the other two. On the other hand, steer 12 shows only a slightly higher percentage than steer 6, but No. 12 had the poorest beef conformation (except No. 9) of the whole herd, which in part accounts for his poor showing in dressed beef, although grain-fed. Perhaps one of the most striking features of this comparison is the very high percentage of dressed beef noted with steers A and B, since, as already pointed out, it was believed that these animals could easily have been fed at least 2 months more and on heavier grain rations to bring them up to standard. As will be seen from the scoring of the animals in Table 59, p. 223, none of them represented what would be called "finished" fat steers, although with several exceptions the grain-feds were well fleshed. In our judgment, also, steers A and B were not in as highly finished condition as either Nos. 4 or 5, so that their higher percentages of dressed beef are a little contrary to expectation, particularly when one considers that these two animals had been upon a submaintenance ration for a very long period and had undergone a measurable loss of 1,300 grams of nitrogen and an estimated

loss of 52 kg. of fat. Apparently, steers A and B naturally carried more flesh under equal conditions but had not progressed so far in laying-on of fat, as indicated by the fact that the amount of internal fat in Nos. 4 and 5 was double that in steers A and B.

Using the percentage of dressed beef as a general index, we can see that although the lowest percentage is noted with No. 9, a grass-fed animal, No. 6, also a grass-fed steer, shows essentially as high a percentage as No. 12 that was fed on concentrates, while with No. 2, which had not been subjected to a submaintenance ration but was grass-fed, the percentage of dressed beef is slightly less than with No. 6. In other words, the conclusion would be that, save in the case of steer 9, the submaintenance ration had not materially influenced the subsequent preparation for market of these animals fed back upon grass alone. It is quite clear from the comparison of the percentages of dressed beef with Nos. 4 and 5 and the other animals, particularly steers A and B, that there was nothing at all detrimental in the prolonged period of undernourishment which would affect the subsequent preparation of the steers for market on concentrates.

### Character of the Dressed Beef.

The mere mathematical expression of the percentage of dressed beef to be derived from a carcass is not, however, the only method of estimating the influence of any previous alteration in feeding régime, for with an equal or even higher percentage of dressed beef the quality of the flesh might conceivably have suffered somewhat by the long period of undernutrition. For example, one animal may show a high percentage of dressed beef, but carry a large proportion of bone, so that it would finally not cut very profitably from a retailer's point of view, while another animal showing the same percentage of dressed beef would carry more flesh and fat and less bone and therefore cut more profitably. Such, in fact, seems to be the case here. Nos. 1 and 9 were especially heavy-boned individuals, while the remainder of the animals were more equally balanced, although no final distinction was made on this particular point by the buyers. Moreover, the condition of the carcasses as differentiated by the amount of fat distributed or infiltrated through the muscle-tissue (which in advanced stages of fattening gives a marbled appearance to the meat in cross-section) is a characteristic that indicates ripeness and palatability, but in a measure quite unrelated to the percentage of dressed beef, as two animals may dress out the same percentage, the one having the fat evenly and finely distributed through the tissue which gives flavor and makes the meat tender, the other having the fat deposited in larger, solid masses, often termed lumpy, which does not improve the quality of the meat.

It was our earnest desire to secure most careful comparative estimates of the various dressed carcasses of these steers, but because of the conditions surrounding the slaughtering, already pointed out, direct comparison of the steers is very difficult. Even the market price makes it possible only to compare animals slaughtered at the same time, and this only imperfectly. The judgments of the several carcasses (1) of Group I at Durham by the professional beef-dresser from Brighton, (2) of Groups II and III after slaughter at Brighton, and (3) of steers A and B after slaughter at Durham, are given in abstract as follows:

*Steer 4.*—The dressed carcass was well fleshed and firm, fairly well marbled, with medium sides; compares favorably with western grain-fed beef.

*Steer 5.*—Carcass well fleshed and firm; fairly well marbled, with medium sides.

*Steer 2 (the grass-fed animal).*—Fairly well fleshed, but with tendency to softness, marbling fair, lacking finish; medium sides.

With regard to the steers in Groups II and III, the carcasses of all the grain-fed steers carried a fairly good covering of fat over the ribs and back. Even Nos. 6 and 9, the grass-fed animals, made an unexpected showing in that the surface was covered with fat, although not with so thick or general a layer as in the case of the grain-fed animals. In general appearance there was not much difference in finish between the various sets of grain-fed animals. All showed good thickness of flesh, although No. 8 showed a slightly better finish, followed by Nos. 3 and 11 in order. The older set of animals, Nos. 1, 10, and 9, had a slightly darker flesh, with almost entire absence of marbling. It is to be noted, however, that No. 9 was a grass-fed animal. No noticeable difference seemed to exist between Nos. 3, 7, 8, 11, and 12 in the marbling. All of these steers showed more fat in the muscle than Nos. 1 and 10, but even these animals were slightly deficient in this respect. After having hung in the cooler for 24 hours, the flesh seemed quite firm on all the grain-fed steers. Nos. 6 and 9, the grass-fed animals, on the other hand, were thin-fleshed and failed to hold a firm shape after cooling because of the deficiency of flesh to support it. The carcasses of steers A and B presented a very marked contrast with each other. Steer A was better fleshed generally and carried a much heavier covering of fat over the carcass generally.

### Comments of Buyers on the Carcasses of the Steers in Groups II and III.

The comments of the buyers could be secured only at the Brighton abattoir. The buyers, mostly Hebrews, were going about in the cooler, selecting the meat which they wanted. The Jewish buyers were interested only in the fore quarters. Several of them remarked, possibly for purposes of barter, that the fat was not properly distributed in the muscle of these animals to make the best-grade meat and that the marbling effect was not present as it should be, that the fat appeared to be more in streaks between the muscles. Some of the men at the abattoir, who were not themselves professional buyers, were questioned with regard to the procedures. They agreed that it would be very difficult to tell from the steer before he was butchered, as he stood on the hoof, just what the quality of the meat would be. They emphasized that while the buyers might be prejudiced and especially critical, realizing that the beef from these animals had come through a different routine than it commonly followed, they had a high degree of skill in judging the quality of the meat. Consequently, based upon the judgment of the buyers, these men did not believe the quality in this case was of the very best.

It is extremely unfortunate that a more competitive form of judgment of this beef from the various buyers was not possible. The conditions of slaughtering, the long delay in the stockyards, the shrinkage (which was undoubtedly considerable), the psychical effect upon the buyers of knowing that the meat was the result of an experiment or test, all militated against the best judgment of this beef.

### Price Indices.

Although the sale and slaughter of these steers occurred on three widely separated dates and represented three distinctly independent or separate market conditions, certain light is thrown upon the relative values of these steers by the prices paid for the dressed meat. The prices, however, can serve for a comparison only between the individual animals sold on the same date. The financial returns on dressed beef for Group I, slaughtered in August 1919, show that steer 2 (grass-fed) brought 12½ cents per pound on dressed sides while steers 4 and 5 (grain-fed) brought 14 cents per pound on dressed sides. In Groups II and III, slaughtered November 1919, the grass-fed steers, Nos. 6 and 9, brought 13 and 12 cents, respectively, for dressed sides, while the grain-fed steers brought 16½ cents, no discrimination being made between individuals. The difference between the price for grass-fed and grain-fed steers was, therefore, measurably less in Group I than in Groups II and III. This is partly accounted for by the fact (1) that steer 2 was in somewhat better condition than steers 6 and 9, (2) that steers 4 and 5 were not quite so well finished as the grain-fed steers in Groups II and III, since the latter had been fed grain over a much longer period, and (3) that when Groups II and III were slaughtered the market level was somewhat better than when Group I was slaughtered. The matter of the sale price of Groups II and III is complicated somewhat, however, by the fact that it was necessary to cut the dressed sides to take photographs (which are not reproduced here), and concessions in price were demanded by the buyers for cutting the dressed carcass into parts for photography. However, on the scale of prices it can be seen that the grass-fed steers in general brought measurably less than the grain-fed steers. This indicates that the carcasses of the grass-fed steers were quite inferior to those of the grain-fed steers.

## GENERAL SUMMARY.

1. Based upon the feeding habits of wild animals, whose supply of feed is, by virtue of the influence of climatic and seasonal changes, subject to great alterations, and based upon the extensive laboratory experiments made on men, who voluntarily submitted to a great reduction in diet for many months, 11 adult steers (Groups II, III, and IV) were subjected for a period of about 4½ months (under constant supervision and with controlled feeding) to a great reduction in ration amounting to approximately one-half or more of their maintenance requirements. During the same period 3 other steers (Group I) were studied as control animals, being accorded exactly the same barn treatment but receiving sufficient hay to maintain them at nearly constant body-weight. Subsequently, 11 of these steers received fattening rations of hay and concentrates, while 3 were put on pasture.

2. A special respiration chamber with novel aliquoting device was designed, constructed, and used to determine periodically the gaseous metabolism, specifically the carbon-dioxide production of the steers at the different nutritive levels. Graphic records of the degree of repose of the animals accompanied each respiration experiment. Determinations were made of the composition of the hay and different grains, and with 2 of the steers (Group IV) more detailed analyses were made of the composition of the feed and feces and the nitrogen in urine.

3. The daily fluctuations which occur in body-weight, even when the feed consumed is quantitatively and qualitatively constant, are of such magnitude (due largely to irregularity in consumption of water and retention of feces and urine) that live weight can be accepted as an index of increase in body-tissue only with the greatest degree of reserve. When the period of observation is short, the intake of feed and water and the visible excreta must be measured for intelligent interpretation of live-weight values, and when the period of observation is long (i. e., 3 to 6 months, as is the case in general feeding experiments), from 5 to 10 daily weighings under carefully controlled conditions as to time of feeding, watering, and weighing, should be averaged to represent the true probable weight. But even this procedure simply corrects for probable daily variations in fill at the time and does not correct for the discrepancy between the fill at the beginning of a fattening period and that at the end, when the character of the fill is often vastly different in its crude-fiber content and in its probable water-holding capacity. The effect of curtailing rations from what constituted approximately maintenance to one-half that amount over a period of 135 to 140 days caused a loss with all the steers of approximately 23 per cent in live weight, the greater part of this loss having taken place during the first month or 6 weeks. During the last few weeks of undernutrition the weights of all the submaintenance animals except steers A and B (Group IV) remained essentially at a constant level or plateau. On doubling the quantity of hay for a week or two following the submaintenance period the live weight increased, the rate of increase corresponding to the rate of decrease noted for a short period just after the reduction in feed. Since in the first week or two of realimentation the feed was composed solely of hay, the caloric increase in the hay ration on refeeding

could not have accounted for a deposition of fat or flesh even approximating the increase in live weight. Hence much of the increase in live weight on the doubled hay ration must have represented increase in fill, and similarly much of the loss in live weight following ration curtailment must have been due to a decrease in fill. Body-measurements of some of the steers taken during the transition stages, particularly circumferences at chest, paunch, and flank, strongly support this deduction, since the chest circumference is only negligibly affected by sudden changes in fill, but decreases very slowly when the feed cut is carried over a long period, whereas the paunch and girth show marked variations simultaneously with variations in feed and fill. The two steers put on pasture following the undernutrition period regained their original weight in almost one-half the time required by the other steers, but here again the sudden increase is to be explained by increased amount of succulent fill.

4. A pronounced decrease in chest circumference (measured just back of the elbow) was noted with all the steers at the end of the submaintenance feeding, and the reduced girths remained at a fairly constant value for several weeks after realimentation began. Thereafter there was a slow but constant increase in the measurement until the end of the fattening period. The fact that on refeeding our steers only slowly began to show an increase in the chest-girth, although at the same time their increase in weight was relatively enormous, is further evidence that the change in weight at first was in large part due to fill and not to the deposition of organized body-tissue.

5. Experimentally, water forms one of the most potent causes of error in the study of nutrition problems, due primarily to the irregularity in the quantity consumed from day to day, but also because of the great variability in quantity retained by fill or in circulation by rations differing in quantity and character. While the amounts consumed from day to day varied enormously (ranging within limits of 0 to 80 kg.), the relationship of water intake to the intake of water-free substance in feed was found in the case of all the steers in Groups I, II, and III to be close to 2.5 kg. of water for every kilogram of water-free substance in feed, but 3.0 kg. and over in the case of Group IV. This ratio was, however, with all the steers lower in general than the commonly accepted value of 4 or 5 kg. of water per kilogram of water-free substance in feed. Since water serves as the principal vehicle of transportation of matter within the animal organism, it has three chief uses: (1) softening and preparing of food material for digestion, (2) flushing of the digestible material through the tissues; (3) as carrier for flushing out waste products, namely, nitrogen in urine, and undigested feed residues in the intestinal tract. The avenues for its elimination from the body are the intestinal tract, the urinary tract, the respiratory system, and by evaporation from the skin. While the amount of water consumed seems closely proportional to the water-free substance in feed consumed, the amount eliminated by each of these avenues of escape varies with unlike amount and quality of feeds. The general observations are, however, (1) that the amount of urine is but little affected when the ration is increased quantitatively (inducing thereby an increase in consumption of water), since the excess water needed for flushing the increased amount of digestible material absorbed through the tissues is eliminated largely as water-vapor through the lungs and skin, (2) that highly nitrogenous rations do stimu-

late a larger secretion of urine; and (3) that the amount of water carried off with undigested feed residues in the intestinal tract is in general proportional to the amount of water-free substance to be eliminated, the water serving largely as a mechanical means for this process

6. During the submaintenance periods the feces of all the steers were of a distinctly harder form, in smaller masses, and drier. When fattening rations were given the fecal excretion became very large, the weights of feces during this time being remarkably constant from day to day. Water consumption had a very marked effect on the feces, a low water consumption resulting in drier and darker feces on the following day and a large consumption of water resulting in somewhat softer feces, and yet analyses showed differences of but 2 or 3 per cent in moisture. The energy of the feces of steers A and B was remarkably constant under all feeding conditions, being on the average in the hay periods 4.778 calories per gram of water-free substance, or in both the hay and grain periods 5.210 calories per gram of water-free and ash-free substance. These factors may serve for computing the energy of water-free and ash-free feces, respectively.

7. With Group IV there was a somewhat higher digestibility of water-free substance in feed on the low hay ration than during the one period of supposedly full maintenance, but in general the profound curtailment of the hay ration did not measurably affect the coefficients of digestibility and the conclusion is that the digestibility of a single feedstuff like hay, constituting the sole ration, is practically unaltered either by the amount of hay fed within wide limits, or by the nutritive plane of the animal.

8. Relatively enormous changes in the amount of drinking-water had little, if any, influence upon the weights of urine, when the steers were upon a constant hay ration. With a ration of hay alone the amounts of urine were practically unaltered, irrespective of the amount of hay given. The regulatory mechanism determining the quantity of urine excreted is apparently unaffected by daily amounts of nitrogen up to 90 grams per day. During the fattening periods there was little change in the urine excretion of steer A, but with steer B there was a marked increase in the weight of urine which was coincidental with the larger amounts of nitrogen in his feed and the greater digestibility of nitrogen.

9. The quantities of nitrogen metabolized were very low in the periods of submaintenance. Thus, the total daily nitrogen excretion of steers A and B (with an average body-weight of about 450 kg. and on a submaintenance hay ration containing 3.6 kg. of water-free substance per day) was about 22 to 24 grams or 45 to 50 mg. per kilogram of body-weight.

10. During the so-called "maintenance" periods it was found that it was impossible to secure nitrogen equilibrium with hay alone and that probably 300 or 400 grams of concentrates per day should have been given, with probably somewhat more than the supposedly "maintenance" amount of hay. During the submaintenance periods there was a consistent loss of nitrogen (about 1,300 grams on the average for steers A and B), but during the fattening periods there were heavy additions of nitrogen to the body, which were practically sufficient, if expressed in the form of flesh, to account for the entire gain in weight observed with these steers during this time. With steer A the storage of each gram of nitrogen necessitated the ingestion in the form of hay

and grain of 6 grams of nitrogen and with steer B (on a ration richer in protein) of 8 grams of nitrogen.

11. During the first week or two of undernutrition the steers showed increased restlessness and craving for bulk in their feed, but after the digestive tract had become adjusted to the quantitative change in contents they were not so restless. Reduction in feed had a marked effect on the frequency of rumination, the steers with lowest amounts of feed ruminating very little. In general, the steers on submaintenance rations moved around more slowly and with less vigor than the control steers, but apparently showed a desire for exercise. In an open lot they showed astonishing energy and activity for animals on such supposedly weakening rations.

12. Reduction in feed caused a very marked shrinkage of the paunch. The hair lost luster and the skin became drier and tended to adhere more closely.

13. There is no clear evidence that undernutrition has any effect upon the rectal temperature, as there was apparently no change in the rectal temperature during the submaintenance periods.

14. Skin-temperature measurements made on one day only would indicate that there is probably a slightly higher skin temperature with the better-nourished steers.

15. The pulse-rates of all the steers decreased greatly following the reduction in rations, but during the fattening period were doubled or more than doubled. The correlation between the pulse-rate and the metabolism was very striking, low pulse-rates being found with a low metabolism and, conversely, high pulse-rates usually being coincident with a high metabolism. With 9 of the 14 steers an absolute minimum pulse-rate of 28 beats per minute or below was noted, one steer actually having a pulse-rate on one day as low as 20 beats per minute. The data secured show no correlation between age and pulse-rate or environmental temperature and pulse-rate.

16. It was found impracticable to measure the gaseous metabolism of our steers under probable *basal* conditions, since this would involve the withholding of feed for 2 or 3 days at least. Accordingly the measurements were made under "standard" conditions, i. e., with the steer standing with minimum muscular activity and 24 hours after the last ingestion of feed. A comparison of our standard metabolism values, however, with unpublished data secured by Professor Armsby and furnished us with permission to use, shows that our values for the standard heat-production (obtained during the first 12 hours after 24 hours of fasting) can not in all probability be any more than 12 per cent above the basal metabolism. The carbon-dioxide production alone was measured and the heat computed therefrom by assuming during the periods of hay ration a factor of 3.1 calories per gram of carbon dioxide and during the hay and grain periods a factor of 2.9 calories. These heat factors were based upon unpublished data kindly given us by Professor Armsby.

17. Experiments upon the factors affecting standard metabolism showed that muscular activity could increase the carbon-dioxide production 55 per cent at the maximum, but in general the activity of our steers was such that the metabolism was rarely increased over 15 per cent. Experiments made immediately after the ingestion of moderate amounts of hay indicated that there is no measurable increase in metabolism during the first hour or two after the ingestion of this amount of feed. With fasting continued beyond

24 hours, the evidence would seem to indicate that the carbon-dioxide production continues to decrease, but the decrease is nowhere so great proportionately as that noted during the first 24 hours. Therefore, although the metabolism is on a distinctly sliding scale following the ingestion of feed, we believe that by far the greater part of the fall in metabolism takes place by the twenty-fourth hour and that our selection of a period 24 hours after the last feed for the measurement of the standard metabolism was in all probability as satisfactory as could be made. A comparison of the metabolism during standing and lying, although not very satisfactory, appeared to indicate that the increase in metabolism due to standing is not far from 17 per cent.

18. Within the temperature limits in which we worked there was no uniformity whatsoever between the metabolism and the environmental temperature, and yet there repeatedly appeared evidence that a low temperature was coincidental with a low metabolism and vice versa, a condition strikingly at variance with all previous conceptions of the relationship between the heat-production and environmental temperature.

19. A careful study of the standard metabolism of all the steers during the short period of maintenance feeding at the start showed that rather considerable variations are to be found, but in general the maintenance-level of metabolism was 2,140 calories per square meter of body-surface (computed by Moulton's formula) per 24 hours. With the control steers during the long period of supposedly hay maintenance the standard 24-hour heat-production was nearer 1,820 calories per square meter of body-surface, but there was a distinct tendency for the metabolism to reach the extraordinarily low level of 1,470 calories for about 2 weeks during the latter part of February and the first of March. The evidence is thus for a seasonal variation in standard metabolism.

20. With the 11 steers subjected to ration curtailment, the undernutrition in every instance had a pronounced influence upon the metabolism in that after a few weeks of adjustment the total metabolism was greatly lowered. The lowering of metabolism was independent of loss of body-weight, for similar decreases in metabolism were noted when computed on the basis of uniform weight or per square meter of body-surface. The low level was maintained for several months, until refeeding with hay began, when there was almost immediately a rebound in the metabolism, indeed, an increase not at all proportional to the moderate increase in the metabolizable energy in the ration. With the heavy fattening rations a further increase in metabolism took place. The metabolism of the steers on pasture likewise increased, very rapidly at first, but did not assume the high intensity noted with the grain-fed animals. Steers A and B were exceptions in two respects. With them there was no period of adjustment at the beginning of the submaintenance period, as with the other steers, and their metabolism was on a somewhat higher plane throughout the entire experimental year than was the metabolism of any of the other steers.

21. In general three distinctly different metabolic planes were observed with these steers. Thus, on the maintenance ration of hay alone, the standard heat-production per square meter of body-surface per 24 hours was on the average for the four successive groups respectively, as follows: 2,080, 2,120, 2,120, and 2,310 calories. For the short period on the low level of

maintenance with the control group the general average was 1,470 calories. For the long period of submaintenance, ruling out the period of adjustment at the start, the standard 24-hour heat-production per square meter of body-surface was 1,460 calories on the average for Group II and 1,490 calories for Group III. For the entire submaintenance period with Group IV the general average was 1,670 calories. Finally, during the fattening period the averages for all four groups were, respectively, 2,160, 2,200, 2,210, and 2,230 calories.

22. If one considers that the steers were essentially on the same metabolic plane at the beginning of the period of hay maintenance and at the end of the fattening period, a general average value of 2,150 calories per square meter of body-surface per 24 hours would be not far from representative of the standard metabolism. The all-important fact from the physiological standpoint is that the maintenance-level of 2,150 calories per square meter of body-surface per 24 hours was, as a result of the curtailed rations, lowered in general about one-third, i. e., to 1,475 calories (the average for the low level of submaintenance on hay alone with Groups II and III). That the cell function was not damaged by this protracted undernutrition is brought out by the extreme rapidity of the resumption of the original metabolic level upon realimentation with even moderate amounts of feed.

23. With Group IV on a ration exclusively of hay it was found that the metabolizable energy in the hay amounted on the average to 2,111 calories for every kilogram of water-free substance in the hay, irrespective of the nutritive plane. Larger values were found with the fattening rations, but it did not seem justifiable to average them. These values determined with Group IV were used in computing the metabolizable energy in the feed of steers 1 to 12.

24. A comparison of the metabolizable energy in feed per day and the total 24-hour heat-production of these steers, in an attempt to determine whether they were in energy balance or not during the period of undernutrition, is very unsatisfactory, owing to the lack of evidence as to how closely the standard heat-production as measured represents the total 24-hour energy requirements.

25. From a comparison of the metabolizable energy in the feed, the course of the body-weight curve, the measured standard heat-production, and the nitrogen-balance, it is computed that each of these adult steers, when subjected to a 50 per cent reduction in rations, came through the winter (140 days) with a loss of 1,300 grams of nitrogen and approximately 52 kg. of body-fat.

26. The actual cost in metabolizable energy for each kilogram of body-weight gained during the realimentation period was essentially the same with the steers in Groups II and III (except for the grass-fed steers) as it was with the control animals, Nos. 4 and 5. It is clear, therefore, that the undernourished animals had not sacrificed in any way their ability to lay on flesh, that their physiological functions were in perfectly normal condition, and that the cost in metabolizable energy was no greater than that furnished normal steers put through the fattening process. The lack of any satisfactory means for computing the metabolizable energy furnished to the steers which were put on pasture makes the consideration of the cost of pasture feeding impossible.

27. At the time of slaughter the 3 grass-fed steers were judged to be in a poorer condition of flesh (as was to be expected) than any of the other steers. Two of these grass-fed steers had previously been subjected to submaintenance rations and the third was a control steer which had been previously given a maintenance ration of hay. One of the submaintenance animals recovered its losses on pasture and made as substantial gains as did the control steer on pasture, scoring equally as well when slaughtered. The other, older submaintenance animal failed to make as substantial gains on pasture.

28. Adult steers may be carried through the winter on extraordinarily low rations and subjected to heavy losses in weight without experiencing any permanent damage, and are able to resume their original weight and, indeed, can be fattened for market with subsequent high feeding.

## ADDENDUM.

As this report goes to press a copy of the first extensive presentation[1] of the experimental series with the respiration chamber of Møllgaard has been placed in the hands of one of us (F. G. B.) while on a visit to the laboratory of Professor Møllgaard. In this publication findings are recorded which should be discussed by us. Unfortunately at this time conference between the two authors is impossible and we can here only call attention to this publication, which is the first of a series of reports on the metabolism of ruminants that should now appear regularly. As an indication of the extent of the Danish research in metabolism, it may be stated that we are informed that over 200 experiments in the respiration chamber, each 48 hours in length, have been made up to June, 1923.

[1] Møllgaard, Om Naeringsvaredien af Roer og Byg til Fedning og om Naeringsstofforholdets Betydning for Fodermidlernes Naeringsvaerdi. Beretning 111, Forsøgslaboratoriet, Kobenhavn, 1923, 159 pages. Although printed in the Danish language, this report contains a short summary in English and the column headings in the tables are printed in English as well as Danish.

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